

OSTRACODA AND PALAEOSALINITY FLUCTUATIONS IN THE MIDDLE JURASSIC LEALT SHALE FORMATION, INNER HEBRIDES, SCOTLAND

by MATTHEW I. WAKEFIELD

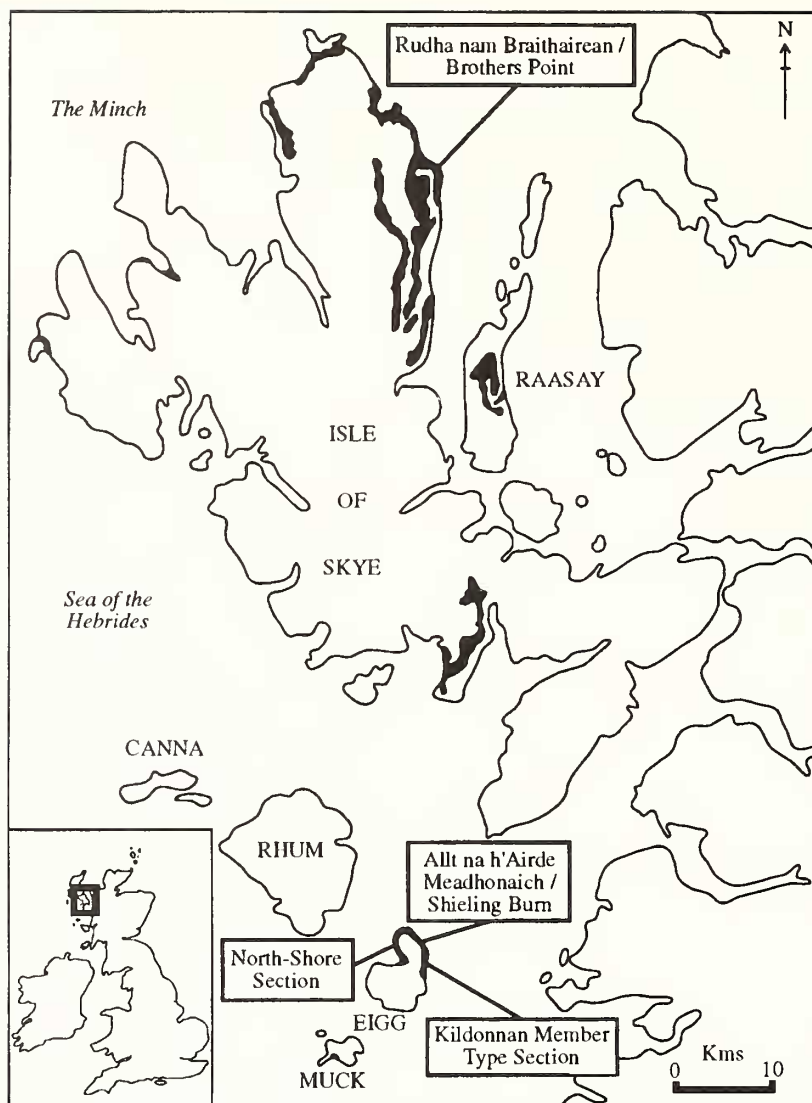
ABSTRACT. Molluscs, conchostracans, algae, palynomorphs and, in particular, ostracods are used to define fluctuating salinities in the Lealt Shale Formation, Great Estuarine Group (Upper Bajocian–Bathonian, Middle Jurassic). Salinities ranged from oligohaline (0.5–5‰) to mesohaline (5–18‰). Fluctuations were often rapid, occurring over only 10–20 mm of sediment. The Kildonnan Member of the Lealt Shale Formation is shown to have experienced a more unstable salinity history than the Lonfearn Member of the same formation. The ostracods are shown to provide a more accurate interpretation of the palaeosalinity fluctuations in the sections studied than do the molluscs. Occasionally only integrated studies allow a reasonably viable determination of palaeosalinity. Salinity tolerance ranges are estimated for 26 ostracod species in the sequence studied. Published oxygen isotope analyses of the mollusc *Praemytilus strathairdensis* are shown to correlate well with the salinity fluctuations determined using the ostracod fauna. High abundances of the fresh to brackish water tolerant alga *Botryococcus* correlate with occurrences of freshwater ostracods (*Limnocythere*, *Theriosynoecum* and *Darwinula*), as well as with freshwater molluscs (*Unio* and *Viviparus*), and with conchostracans.

THE aim of this paper is to elucidate the possible palaeoenvironmental significance of the Ostracoda within the Lealt Shale Formation. The paper determines a relative salinity tolerance for each ostracod species from the Lealt Shale Formation and uses these interpretations to detail the palaeosalinity of the depositional environment. Previous studies on the palaeoenvironment using bivalves, gastropods, conchostracans and algae are tested. By the integration of data from all the available faunal evidence a palaeosalinity curve for each section studied is defined.

THE GREAT ESTUARINE GROUP

The Great Estuarine Group, as defined by Harris and Hudson (1980), is composed of seven formations, all of which were deposited under non-marine to marginal marine conditions (Hudson 1963a, 1966, 1970, 1980; Tan and Hudson 1974; Hudson and Harris 1979; Andrews 1984, 1985; Andrews and Walton 1990). Despite the facies variations manifest in the Great Estuarine Group, the vertical succession is remarkably constant over the entire outcrop, which amounts to c. 90 km in length (Text-fig. 1). Indeed, some individual beds can be traced over the entire outcrop, e.g. the algal stromatolite, which divides the two members of the Lealt Shale Formation, the Kildonnan and Lonfearn members (Hudson 1970, 1980; Harris and Hudson 1980). The Great Estuarine Group has no fully marine sequences within its succession, and, as such, no ammonites with which to date it. A composite dating and correlation (Text-fig. 2) based on palynomorph biostratigraphy, lithofacies correlation and sequence stratigraphy is used to provide a chronostratigraphical framework for the sequence (Wakefield 1991, 1994).

Hudson (1963a, 1966, 1980) and Tan and Hudson (1974) considered that the Lealt Shale Formation was deposited in lagoonal systems which had a direct link to waters of marine salinity;



TEXT-FIG. 1. Location of the outcrop of the Great Estuarine Group (shaded) and of the sections sampled.

an open lagoon in the sense of Hudson (1980). Stable isotope studies (C and O), particularly upon *Praemytilus strathairdensis*, indicate direct seawater–river water mixing (Tan and Hudson 1974, figs 1–2). It was considered that the deposits were not truly estuarine, because this type of environment would not allow the equilibration of ^{13}C with atmospheric CO_2 as required to explain the heavy carbon values found, and also because of the wide lateral extent of this very shallow facies (Hudson 1963a).

SECTIONS STUDIED

The Kildonnann and Lonfearn members (Harris and Hudson 1980) of the Lealt Shale Formation were originally named the Mytilus and Estheria Shales respectively (Anderson 1948; Hudson 1962).

		Ammonite Zones	Ammonite Subzones	Proposed correlation					
Callovian		<i>Macrocephalites herveyi</i>	<i>M. camptus</i>	Staffin Shales Fm	Belemnite Sands Member				
			<i>M. terebratus</i>						
			<i>Kepplerites (K.) kepperi</i>						
BATHONIAN	UPPER	<i>Chydoniceras (Chydoniceras) discus</i>	<i>C. (C.) discus</i>		Upper Ostrea Member				
			<i>C. (C.) hollandi</i>						
		<i>Oppelia (Oxycerites) orbis</i>		Skudiburgh and Kilmaluag formations					
	MIDDLE	<i>Procerites hodsoni</i>		Duntulm Formation					
		<i>Morrisiceras (Morrisiceras) morrissi</i>							
		<i>Tulites (Tulites) subcontractus</i>							
	LOWER	<i>Procerites progradilis</i>		No correlation with standard ammonite zones possible	Valtos Sandstone Formation				
		<i>Asphinctites tenuiplicatus</i>				Lealt Shale Fm.	Lonfearn Member		
			<i>Zigzagiceras (Zigzagiceras) zigzag</i>					<i>O. (O.) yeovilensis</i>	Kildonnan Member
								<i>M. (M.) macrescens</i>	
<i>P. (P.) convergens</i>									
Bajocian	<i>Parkinsonia parkinsonia</i>	<i>P. bomfordi</i>	No correlation with standard ammonite zones possible	Elgol Sandstone Formation					
		<i>S. truelli</i>							
		<i>P. acris</i>							
	<i>Strenoceras (Garantiana) garantiana</i>	<i>S. (G.) tetragona</i>			Cullaidh Shale Formation				
		<i>S. (G.) subgaranti</i>							
		<i>S. (P.) dichotoma</i>							
		Garantiana Clay							

GREAT ESTUARINE GROUP

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TEXT-FIG. 2. Suggested correlation of the Great Estuarine Group with the standard ammonite zones.

The type sections of the formation are exposed on the islands of Eigg and Skye in the Inner Hebrides off NW Scotland. The type section of the Kildonnan Member is exposed 2.5 km north of Kildonnan, Isle of Eigg [NM 495870] (Harris and Hudson 1980); the dominant lithology is grey, silty shales with monotypic shell beds of the bivalve *Praemytilus strathairdensis*. Other distinctive shelly limestones and sandstones are used to correlate the different parts of the discontinuous exposure (Hudson 1966). Harris and Hudson (1980) show that this section ends with an algal stromatolite. The upper beds of this section (as recorded in Hudson 1966), including the top of Bed 8 and the Algal Bed, lay above a low angle slip plane and have now been largely eroded away. It is unlikely that more than a metre of the Kildonnan Member is missing from the top of the exposure, whilst the base of the exposure is considered to be only a couple of metres above the underlying Elgol Sandstone Formation. The transition from the Kildonnan to the Lonfearn Member is exposed in several sections around the north-west coast of Eigg, particularly at NM 469904–475908. The type section of the Lonfearn Member (Harris and Hudson 1980) is a composite of the exposures seen at Rudha nam Braithairean [NG 526625] and the mouth of the Lonfearn Burn [NG 517551]; the typical lithology is dark grey to brown shales, which often appear black due to metamorphism by the numerous Tertiary sills and dykes. The upper portion of the Lonfearn Member was sampled in the Shieling Burn, Eigg [NM 497888]. The top of the Lonfearn Member, and of the Lealt Shale Formation, is defined at the incoming of *Neomiodon*-dominated siltstones of the Valtos Sandstone Formation (Harris and Hudson 1980).

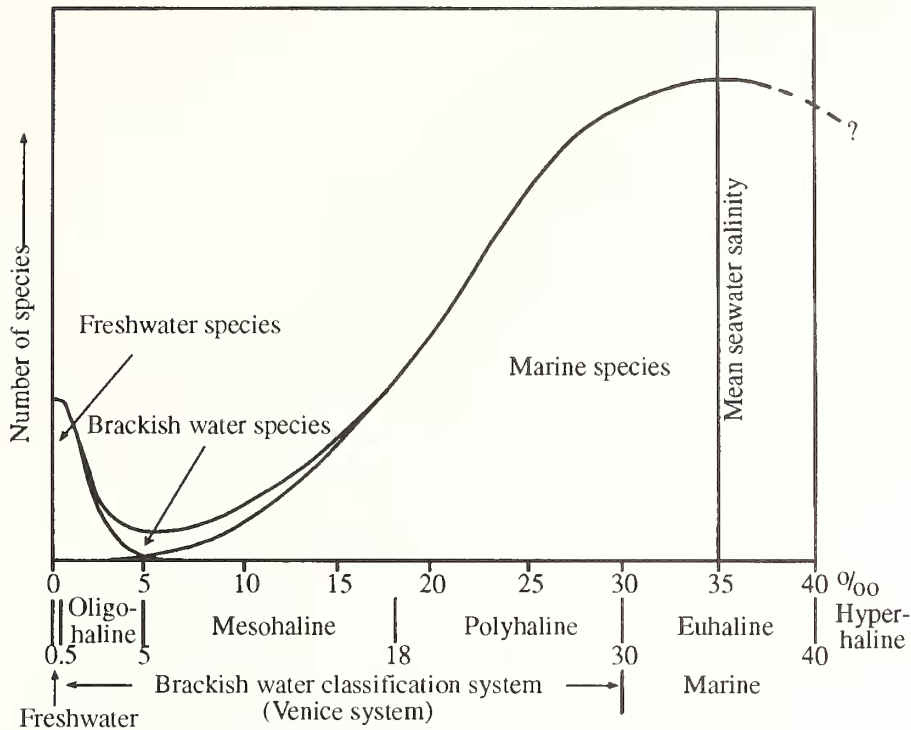
The lithostratigraphical divisions of Harris and Hudson (1980) are used in this paper. The logs for the Lealt Shale Formation sections were supplied by J. D. Hudson, and can be found in the appendix of Wakefield (1991). The logs from the sections exposed on the Isle of Eigg will be published in the 'Small Isles Memoir' of the British Geological Survey (Hudson in press).

SAMPLING AND PROCESSING TO OBTAIN OSTRACODS

Samples each weighing approximately 1 kg were collected from the smallest possible vertical thickness, usually 50 mm. Shales, silty shales, clays, mudstones, silty sandstones and sandstones were sampled. Samples were broken into small, 20–30 mm, sized pieces, half of which were placed in a plastic container and covered with a 10 per cent. solution of H₂O and left overnight. The disaggregated sediment was wet sieved with 2800 μ m, 850 μ m and 125 μ m sieves. These residues were dried, weighed and bagged. Residues were hand picked for ostracods with an 'OO' sable brush using a Wild M8 binocular microscope.

THE CLASSIFICATION OF BRACKISH WATERS

All water bodies are complex chemical solutions of various ions. These give rise to salinity, which in turn may affect the distribution of biotas. Salinity is defined as the total ionic concentration, principally of Na and Cl, and is, therefore, defined in terms of chlorinity (Knudsen 1901). The qualitative terms, freshwater, brackish and marine, of the last century were formally quantified by Redeker (1922), Välinkangas (1993) and finally at the Venice Symposium of 1958. Remane (1934, 1958) documented the abundance of species throughout the freshwater to marine salinity spectrum based upon a hypothetical transect from the North Sea into the Baltic Sea (Text-fig. 3). Chlorinity is not considered to be a good method of assessment of salinity values for those brackish water bodies which have no direct connection to the sea. These water bodies may derive their salinity from solutes other than Na and Cl. These types of brackish water bodies are termed athalassic (DeDecker 1981a). The salinity values and ranges of the Venice system are applied throughout this work. The use of this scale is not intended to imply that Bathonian seawater had a salinity of 35‰, but is used to allow relative changes in salinity to be described.



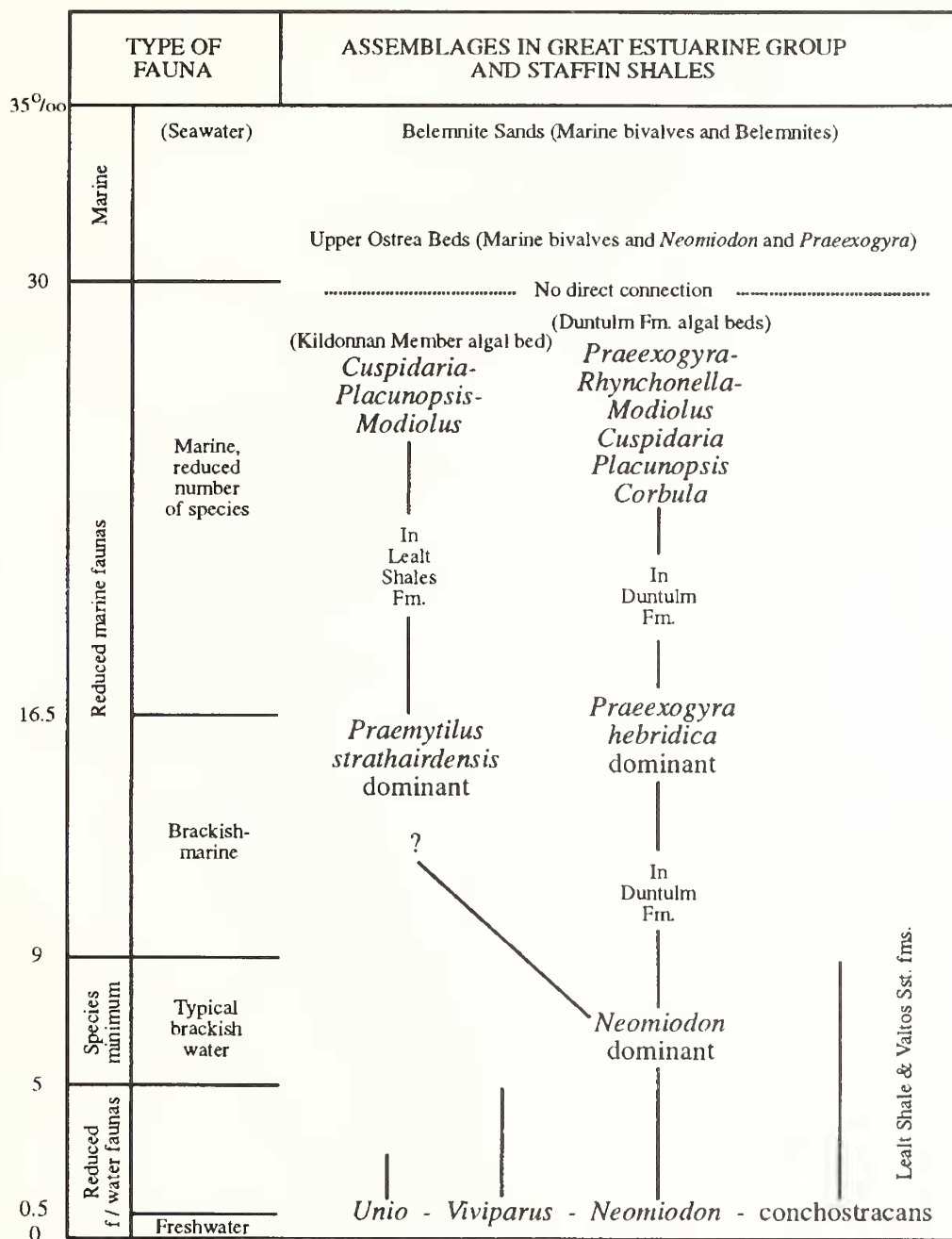
TEXT-FIG. 3. Modified Remane diagram showing the relationship between species diversity and salinity. No precise quantitative significance is implied. The brackish water classification system (Venice System) is shown (after Hudson 1990).

PREVIOUS STUDIES ON THE BIOTA OF THE LEALT SHALE FORMATION

The Lealt Shale Formation is the most palaeontologically diverse formation of the Great Estuarine Group. Studies on the molluscan, conchostracan and algal fauna and flora of the Great Estuarine Group (Hudson 1963*a, b*, 1966, 1970, 1980) were preceded by the publication of faunal lists for the Reptile Bed of the Kildonnann Member (Barrow 1908) and for the Great Estuarine Series (Tate 1873). A faunal list for the Lealt Shale Formation is given in Table 1, which also provides details of species authorship. Hudson (1963*a*) established salinity tolerances for the mollusc and conchostracan fauna and hence recognized salinity fluctuations throughout the Great Estuarine Group. A more detailed account of the palaeosalinity of deposition of the Kildonnann Member type section was included in a paper on Hugh Miller's Reptile Bed (Hudson 1966). Such palaeosalinity studies have been refined over the years by the discovery of pseudomorphs after gypsum in the algal bed from the type section of the Kildonnann Member (Hudson 1970), and detailed by stable isotope studies of, in particular, the molluscs and the algal beds (Tan and Hudson 1974; Andrews 1986). Some of the mollusc species of the Great Estuarine Group also occur in China (Yin 1991). Stable isotope analyses of the Chinese specimens have shown that they lived in waters of comparable isotopic composition, and most probably the same salinity, as did the molluscs of the Great Estuarine Group (Yin 1991).

Hudson (1963*a*) argued for a salinity control upon the molluscan and conchostracans faunas, of which the latter has only recently been described taxonomically (Chen and Hudson 1991). This salinity control was reaffirmed in Hudson (1980). Hudson recognized a series of salinity controlled assemblages (Text-fig. 4), which were based upon associations of molluscs and conchostracans, and made assumptions as to the salinity tolerances of each species. These assumptions relied upon

Darwinula pulmo Wakefield, 1994
Darwinula phaselus Wakefield, 1994
Linnocythere incerniculum Wakefield, 1994
Linnocythere spinosa Wakefield, 1994
Linnocythere melicerion Wakefield, 1994
Linnocythere spannida Wakefield, 1994
Linnocythere ? sp. A. Wakefield, 1994
Linnocythere ? sp. B. Wakefield, 1994
Linnocythere ? sp. C. Wakefield, 1994
Theriosynoecum fimbriachela Wakefield, 1994
Theriosynoecum ramnoscuspis Wakefield, 1994
Theriosynoecum sp. A. Wakefield, 1994
Frons larvata chameleon Wakefield, 1994
Acanthocythere elongata Wakefield, 1994
Acanthocythere ? sp. Wakefield, 1994
Glyptocythere inversalitera Wakefield, 1994
Glyptocythere dextranovacula Wakefield, 1994
Glyptocythere sutherlandi Wakefield, 1994
Glyptocythere shielingensis Wakefield, 1994
Progonocythere milleri Wakefield, 1994
Paracypris ? sp. A. Wakefield, 1994
Aalenella cuneata Wakefield, 1994
Lophocythere sp. A. Wakefield, 1994
Asciocythere pactilis Wakefield, 1994
Praeschuleridea ? sp. A. Wakefield, 1994
Procytherura ? sp. A. Wakefield, 1994



TEXT-FIG. 4. Salinity controlled mollusc and conchostracan assemblages of the Great Estuarine Group and Staffin Bay Shales (modified after Hudson 1963a).

conservatism of the fauna. The co-occurrence of the bivalve *Unio andersoni*, the gastropod *Viviparus scoticus* and conchostracans, contemporaries of which are all known from fresh and oligohaline waters today, supports the initial assumptions. These low salinity forms rarely occur with the bivalve *Praemytilus strathairdensis*, which is considered to be tolerant of mesohaline waters, and

never with the marine bivalves *Placmopsis socialis* and *Cuspidaria ibbetsoni*. Hudson was able to define salinities for the molluscs that he had recorded:

Unio-Neoniodon-Viviparus – 0–3‰.

Neoniodon brycei as only mollusc = species minimum – 5‰; otherwise euryhaline and highly opportunistic.

Praemytilus strathairdensis – lower limit 6–10‰; marine euryhaline; beds which are dominated by small specimens are interpreted as representing the lower end of the tolerance range.

Placmopsis socialis – marine, euryhaline around 30‰.

Cuspidaria ibbetsoni – marine, euryhaline around 30‰.

These salinity ranges have been corroborated by stable isotope analyses of shells from the various molluscan species (Tan and Hudson 1974). Isotopic analyses of *Praemytilus strathairdensis* from Bed 5 of the Kildonnan Member type section by Tan and Hudson (1974) indicated a mean temperature of growth of 22 °C. This figure was later refined to take into account the likely composition of an ice free Earth, producing a figure of 17–18 °C (Hudson 1980). It was argued that the annual mean water temperature was lower because shell growth had only occurred during the warm summer months, as indicated by detailed shell structure work (Hudson 1968). Tan and Hudson (1974) concluded that *Praemytilus strathairdensis* lived in waters whose salinity was determined by variable mixing of fresh and seawaters giving a direct ^{13}C – ^{18}O correlation. When the palaeontological evidence is compared with the life cycle of a typical Recent mussel, such as *Mytilus galloprovincialis* Lamarck, then similarities are evident. Based on detailed life cycle studies, given a summer temperature of 18 °C, then a salinity of 20–25‰ would provide the optimum environmental conditions for growth. The adults of *Mytilus galloprovincialis* are able to survive in salinities as low as 10‰ (Hrs-Brenko 1978).

Recent palynological investigations of the Great Estuarine Group (Walton 1988), have helped to endorse the salinity groupings of the mollusc and conchostracan fauna defined by Hudson (1963a). Walton (1988) found an excellent correlation between high abundances of the fresh to brackish water tolerant planktonic alga *Botryococcus*, the occurrence of the bivalves *Unio andersoni* and *Neoniodon brycei*, the gastropods *Viviparus scoticus* and *Valvata* sp., and conchostracans which were all considered to be tolerant of freshwater (Hudson 1963a). Whilst occasionally abundant with the brackish water tolerant bivalve *Praemytilus strathairdensis*, *Botryococcus* was rare in samples which contained the marine-brackish tolerant bivalves *Tancredia gibbosa*, *Placmopsis socialis* and *Cuspidaria ibbetsoni*.

The mollusc and conchostracan fauna has been used to determine the palaeosalinity of the Great Estuarine Group as a whole (Hudson and Harris 1979). The Lealt Shale Formation was interpreted to have been deposited under variable but generally low salinities (brackish-marine to freshwater). Beds 1–3 of the Kildonnan Member type section, were interpreted to have been deposited under low (fresh–oligohaline; 0–5‰) but variable salinities (Hudson 1966). Bed 5, dominated by the bivalve *Praemytilus strathairdensis*, experienced low brackish-marine salinities (16‰). Beds 6–7 record a general decline in salinity to possibly freshwater conditions in the *Unio* Bed (7a). An increase in salinity is recorded in beds 8–9. The discovery of pseudomorphs after gypsum in the Algal Bed (Hudson 1970, fig. 3) indicates that salinities were hypersaline, at least at times.

Palynological studies of the Great Estuarine Group have only recently been completed (Walton 1988; Riding *et al.* 1991). A brief summary of this work is included to allow a more complete assessment to be made of the Lealt Shale Formation. Only the Kildonnan Member type section and the Lonfearn Member at Rudha nam Braithairean were examined in these works.

In the Kildonnan Member, Riding *et al.* (1991) recorded high levels of gymnosperm pollen; constituting up to 85 per cent. of the palynoflora. The majority of the palynomorphs recorded are non-marine forms. Excepting Beds 6b and 6f, *Botryococcus* was present in almost all samples. Acanthomorph acritarchs, which appear to have tolerated reduced salinities (Walton 1988), occurred with the bivalves *Placmopsis socialis* and *Cuspidaria ibbetsoni* and with marine dinoflagellate cysts. The acritarchs comprised 44.7 per cent. of the palynoflora in Bed 6f. The low diversity dinoflagellate cyst associations are considered to be indicative of marginal marine conditions which were subject

to salinity fluctuations (Riding *et al.* 1991). The Algal Bed contains the highest proportion of pollen, some 97.3 per cent. of the palynoflora.

Botryococcus is ubiquitous in the Lonfearn member. Dinoflagellate cysts occur only occasionally, indicating temporary establishments of marginal marine conditions. The lower abundances of pteridophyte spores, compared with those in the Kildonnan Member, suggests that the land areas were less densely vegetated or further away (Riding *et al.* 1991).

Using the palynofloras, Walton (1988) interpreted the Kildonnan Member type section in the following way. Beds 1–6a (inclusive) were deposited under non-marine brackish conditions. Beds 6b, 6c and the base of 6d had a marine influence (acritarchs). The top of Bed 6d records freshwater conditions (*Botryococcus*). Marine influences (acritarchs) are present in Beds 6e and the base of 6f. A return to freshwater conditions is recorded from the top of Bed 6f through Bed 7a. This interpretation compares well with that given in Hudson (1966) and reported earlier in this review.

Little attention has been given to the ostracod fauna from the Lealt Shale Formation. F. W. Anderson (*in* Hudson 1963a, p. 324) noted that the ostracod fauna was dominated by metacypriids. At this time metacypriids were considered to be members of the Limnocytheridae Sars, 1925, and were subsequently raised to subfamily status (Danielopol 1965). Metacypriinae is now considered to be a junior synonym of Timiriaseviinae Mandelstam, 1960, a view with which I agree (see Colin and Danielopol 1978, 1980 for a review of the systematics of the Limnocytheridae). Taking the above into account, and the similarities in external morphology of *Metacypriis* Brady and Robertson, 1870 and *Theriosynoecum* Branson, 1936, I consider that Anderson was most probably referring to *Theriosynoecum*. Indeed, many synonymies of *Theriosynoecum* contain species originally assigned to *Metacypriis* (see Branson 1966 for examples). However, in Hudson (1966). Gramann and Hiltermann identified, mostly to generic level, ostracods from Bed 3c (*Fuhrbergiella* n. sp.), Bed 5 (*Glyptocythere* cf. *tuberosa* Brand and Malz; *Glyptocythere* (?) n. sp.; *Progonocythere polonica* Blaszyk; and *Progonocythere* n. sp.), and Bed 6b (*Progonocythere* n. sp.). The occurrence of *Glyptocythere* cf. *tuberosa* remains unsubstantiated. It is considered that *Glyptocythere* (?) n. sp. is equivalent to *Glyptocythere inversalitera*, *Progonocythere* n. sp. is equivalent to *Progonocythere milleri*, and that *Fuhrbergiella* n. sp. is equivalent to *Fronsleravata chamaeleon*. No palaeoecological interpretation was given for these ostracods.

Only a single foraminifer species has been reported from the Lealt Shale Formation, namely *Anmodiscus tenuissimus* from Bed 6b, Kildonnan Member type section (Hudson 1966). This occurrence can now be extended to include Bed 6 of the Kildonnan Member of the North Shore Section, Eigg and from the basal 150 mm of Bed 3 of the Lonfearn Member from Rudha nam Braithairean, Skye. *Anmodiscus tenuissimus* occurs with conchostracans, the bivalve *Neomiodon brycei* and occasionally with small specimens of the bivalve *Praemytilus strathairdensis*, and, as such, it is here interpreted to have been tolerant of low salinity brackish waters (oligohaline to mesohaline; 0.5–10‰).

Chen and Hudson (1991) recorded six species of conchostracan from the Lealt Shale Formation (see Table 1). They are interpreted to have tolerated low salinities (Hudson 1963a) which are below those usually occupied by the bivalve *Praemytilus strathairdensis*. Recent conchostracans tolerate fresh and slightly brackish waters whilst growing and breeding, although they commonly inhabit temporary pools (Tasch 1987).

All of the palaeontological research on the Lealt Shale Formation undertaken to date has substantiated the conclusions of Hudson (1963a, 1966), that the formation was deposited under low but fluctuating salinities. It was these salinity fluctuations that appear to have been the major environmental control upon the faunal and floral occurrences.

DETERMINING THE AUTOCHTHONEITY OF OSTRACOD ASSEMBLAGES

Because of the discontinuous growth of ostracods, it is possible to determine the autochthoneity of ostracod assemblages. Most benthic ostracods pass through eight moult stages (instars) between

hatching and maturity. In so doing the ostracod must shed its rigid calcareous valves, and thus leaves a record of its ontogeny for posterity. For each species a record of the moult stages present within a bed gives an insight into the energy conditions of deposition (Whatley 1983, 1988). Each ostracod is measured and plotted on a length:height graph. This allows the different moult stages to be determined. Histograms of the numbers of each moult stage, the age structure of the assemblage, are then used to determine autochthoneity. Sediments deposited under low energy conditions contain ostracod assemblages composed of adults (both dimorphs if present in a particular species) and even the smallest juvenile stages. Due to the large differences in size and hydrodynamic properties of the adults and juveniles, it is unlikely that a low energy thanatocoenosis, as described above, could be constructed by the sequential influences of different hydrodynamic conditions. These types of assemblage are commonest in lacustrine environments (Whatley 1988). Environments with higher energy levels contain ostracod assemblages with incomplete age structures; often only the adults and largest juveniles are present. This age structure is referred to as a high energy thanatocoenosis. Age structures between the extreme end members described above can also be found. These are produced by intermediate energy levels. Allochthonous assemblages often contain only the smallest juvenile stages (Whatley 1983, 1988). As a general rule the smallest juveniles are transported over greater distances than the larger juveniles and adults.

The determination of autochthonous assemblages, as describe above, is further complicated by the preservational state of the ostracods. Oertli (1971) concluded that large numbers of ostracod carapaces within an assemblage indicated a high sedimentation rate. This generalization is overly simplistic and ignores the possible presence of interstitial ostracods, low energy conditions, burrowing habits employed to follow the water table during droughts (DeDeckker 1981b), or of ostracods washed above mean water level during storms (Wakefield 1991). Whatley (1983) noted that ostracods disarticulate their valves during moulting, and that juvenile carapaces indicate infant mortality. The absence of carapaces probably indicates some transport rather than a complete lack of infant mortality. Post mortem carapace preservation depends on hinge structure, valve overlap and whether the adductor muscles contract or relax upon death.

In shallow lagoonal environments, such as those envisaged for the Lealt Shale Formation (Hudson 1963a, 1966, 1980), energy levels would have generally been low. Being so shallow, the environment would easily be influenced by storms. This may explain the lack of the smallest juveniles in the ostracod assemblages studied. Assemblages with adults and a large number of juveniles are common. Assemblages different from this are the exception, some of which have been ascribed to storm deposition (Wakefield 1991). It is these storm-induced mass mortality assemblages which contain large numbers of adults and larger juvenile carapaces, probably as a consequence of rapid sedimentation.

It was not always possible to obtain a large enough number of specimens for accurate age structure studies to be attempted. This was because of variation in the preservation of the ostracods, both within and between sections, as a result of local variation in metamorphism by Tertiary sills and dykes. This was particularly evident in the sections at the Shielling Burn, Eigg, and Rudha nam Braithairean, Skye. For example, calculated recoveries of ostracods per kg of sediment from the Rudha nam Braithairean section varied between a maximum of 18250 and a minimum of 620. These two samples contained the same assemblage (*Limnocythere incerniculum* and *Darwinula pulmo*), with 88–93 per cent. of the ostracod fauna being *Limnocythere incerniculum*. Observations of bedding planes from these horizons indicate that ostracods were equally abundant. It appears, therefore, that variations in preservation are compounded during processing such that many specimens may be effectively destroyed. It was, therefore, in some instances necessary to determine *in situ* ostracods in another way. By counting the number of specimens of each species in an assemblage (each valve represents half a specimen and each carapace one specimen) it was possible to calculate the percentage compositions of each assemblage. In most instances two or three species dominated the assemblage, making up over 80 per cent. of the assemblage, and were considered most probably *in situ*. A qualitative visual check of bedding plane assemblages was carried out at the same time as the counting in order to assess whether adults and juveniles were present for each

species. If only juveniles were present then it was possible to question whether or not the species was *in situ*. Within the Kildonnan Member, and particularly with *Linnocythere incerniculum*, it was noticed that the adults were more prone to damage during processing than the juveniles. This fact exacerbated the problem of determining whether a species was *in situ*. When this method was tried on samples that also had age structure studies carried out, the *in situ* species determined by each method were the same.

OSTRACOD PALAEOECOLOGY OF THE LEALT SHALE FORMATION

Controlling factors on ostracod distribution

Although it is well known that various physical and chemical environmental variables influence ostracod distribution, e.g. climate, water temperature, water depth, substrate, food supply, salinity, pH and oxygen concentration, it would appear that salinity is most likely to have been the primary controlling factor during deposition of the Lealt Shale Formation.

Most of the variables listed above are considered to have had a negligible affect upon ostracod occurrences in the Lealt Shale Formation. The palaeolatitude has been calculated to have been about 35° N (Smith *et al.* 1973). The climate was warm, with mean annual water temperatures around, or slightly below, 17–18 °C (Hudson 1980). It was wet and there was marked seasonality (Tan and Hudson 1974; Hudson and Harris 1979). It seems highly unlikely that these would have varied across the Hebrides depositional basin, around 90 km from north to south.

The water was probably around 5 m deep (Hudson and Andrews 1985). Water temperature is considered not to have varied with depth because of the shallow nature of the environment (Hudson 1963a; Hudson and Andrews 1987). Numerous shell lags attest to a periodically mobile water column as does the winnowed concentration of bone material in the Reptile Bed (Bed 2) of the type section of the Kildonnan Member (Hudson 1966). The *Praemytilus* in shell beds are often orientated, and were probably deposited in the waning ebb flow after storms. Water movement in shallow environments is likely to disrupt the development of a thermocline. The same process will also prevent the development of salinity stratification, a halocline, (Barnes 1980). A mobile water column also suggests that the water was well oxygenated. Ostracod age structure studies suggest only limited and infrequent transportation of valves. Within the Kildonnan Member some assemblages of the ostracod *Linnocythere incerniculum* have been recorded with both sexual dimorphs and usually five and in one instance seven juvenile stages preserved, indicating stable water conditions and autochthoneity of the assemblages. Only the smallest juveniles have been winnowed out. In other samples containing the same species only juveniles were recorded. These may be low energy thanatocoenoses (see above). All of the ostracods present in the Lealt Shale Formation are considered to have been benthic, e.g. *Darwinula stevensoni* (Brady and Robertson, 1870) is known from Recent ecological studies to be benthic, living either on or in the top 10 mm of sediment (Ranta 1979). For benthic ostracods the substrate is likely to have had an important influence on their distribution. However, no variation of species with differing sediment type was noted in either member of the Lealt Shale Formation. Limestones were not sampled, though shales, silty-shales, clays, mudstones, siltstones, silty-sandstones and sandstones were. Plants are also known to affect the distribution of ostracods (Whatley and Wall 1975). It is not possible to determine exactly what plants, or organic detritus, were present in the Lealt Shale environment on which the ostracods could have lived, and/or fed. Large amounts of organic material are preserved in the shales so food was probably plentiful.

Although *Linnocythere*, *Darwinula* and *Paracypris* all have Recent representatives, the environmental preferences of which can be utilized in palaeoenvironmental studies, most Mesozoic ostracod genera do not. As a consequence, most palaeoecological interpretations of Mesozoic ostracods are based upon morphological similarities with related Recent genera, as well as sedimentary and stable isotope geochemical evidence. Benson (1959) thought that 'most genera are too all-inclusive for detailed ecological work' and that it was 'better to use species...for any paleoecological interpretations'. Sandberg (1965) recognized a small number of genera as

being characteristic of brackish water and consequently placed greater emphasis on the use of genera for palaeoenvironmental and palaeosalinity reconstructions. The large number of ostracod species (eleven from eight genera in the Kildonnán Member and fifteen from ten genera in the Lonfearn Member), and the co-occurrences of species enabled an accurate assessment of relative salinity tolerances for the Lealt Shale Formation. No ostracod species occurs in both the Kildonnán and Lonfearn members, so it is not possible to compare directly the salinity tolerances of species from both members. It was decided not to use the mollusc salinity tolerances of Hudson (1963a) as a basis for defining the relative tolerances of the ostracods, in order to allow an independent determination from the ostracods. However, comparisons with the molluscs were used as a means of checking the relative tolerance ranges of the ostracods detailed below.

DETERMINATION OF RELATIVE SALINITY TOLERANCES

Before construction of a salinity tolerance range chart of the Lealt Shale Formation ostracods was attempted, it was necessary to determine which species co-occurred *in situ* (see above). In addition, assumptions were made as to the salinity tolerances of the genera *Theriosynoecum*, *Linnocythere* and *Darwinula*, in order to allow an initial framework upon which to build the relative tolerances of the other ostracod genera and species. It is not possible to determine precise synchronicity in the fossil record, therefore all of the species in a single sample were considered to be synchronous unless evidence to the contrary was available, e.g. as in Bed 3h from the type section of the Kildonnán Member (see below).

The assumption of salinity tolerances for *Theriosynoecum*, *Linnocythere*, and *Darwinula* was based upon studies of both Recent and fossil species. A maximum and a minimum tolerance was assumed for each genus, outside of which it was considered unlikely that the genus could feed, respire and breed. It is known that some ostracods can tolerate enormous variations in salinity, but can only feed and breed over a relatively narrow salinity range (DeDecker 1981a). This assumption of tolerance ranges was not rigorously applied, such that every species of *Linnocythere* had the same tolerance limits. In some cases, it was possible to determine that one species of *Linnocythere*, by its association with ostracods determined to tolerate higher salinities, and the lack of association with another species of *Linnocythere*, had a different tolerance range to the latter species. However, both species' tolerance ranges lay within the generic tolerance range.

These three genera were chosen because they are all either known, or considered to be tolerant of fresh water, and as such only their upper salinity limits vary. Evidence is available to indicate these upper limits with a reasonable degree of certainty. Many of the genera from the Lealt Shale Formation, e.g. *Glyptocythere*, *Acanthocythere* and *Lophocythere*, are considered to have been euryhaline marine. As such both the upper and lower limits of their salinity tolerance could be in doubt.

Salinity tolerance of Theriosynoecum

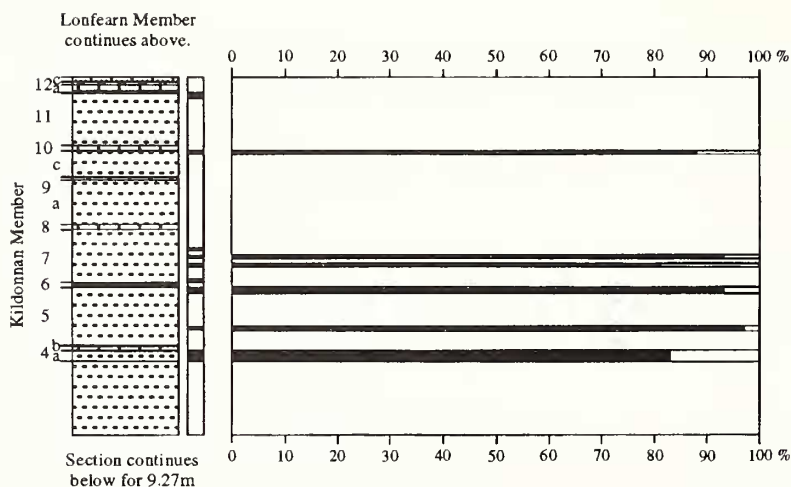
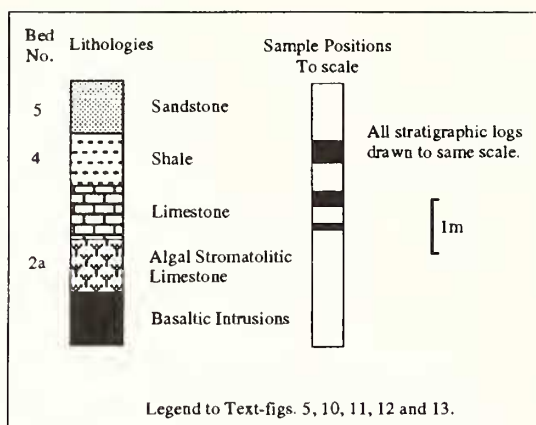
Theriosynoecum is known only from the fossil record, having become extinct in the Albian (Cretaceous; Colin and Danielopol 1979). The majority of the evidence as to its salinity tolerance is essentially inference, and often circular, being based upon its association with other assumed freshwater organisms, e.g. *Darwinula* (see below), charophyte oogonia, conchostracans, the bivalve *Unio* and the gastropod *Viviparus*. In this context it should be noted that a Recent charophyte, *Lamprothamnium papulosum* (Wallroth, 1833), has been found growing in saline waters, and still fixing CO₂ up to salinities twice that of seawater (Burne *et al.* 1980). Most charophytes, however, are regarded as being indicative of freshwater. *Gomphodella* is regarded as the closest related, morphologically similar genus to *Theriosynoecum*, and has an upper salinity tolerance of 2.3‰ (DeDecker 1981b).

Only Kilenyi and Allen (1968) give an inferred salinity range for *Theriosynoecum*. Their study of Purbeck and Wealden Ostracoda, following on from the faunicycle investigations of Anderson

et al. (1967), indicated a range of 0–7‰. Some ambiguity as to the salinity tolerance of *Theriosynoecum* has arisen during the study of the Purbeck and Wealden Ostracoda. Anderson *et al.* (1967) classify *Theriosynoecum* as an S-phase but primarily brackish water genus. Barker (1966) and Kilenyi and Allen (1968) noted that many of the S-phase genera (*Theriosynoecum*, *Klicana*, *Darwinula* and *Rhinocypris*) also occurred in the freshwater C-phase *Cypridea* assemblages. This indicated that these genera were probably tolerant of fresh to oligohaline waters (0–5‰). Kilenyi and Neale (1978) considered *Theriosynoecum fittoni* (Mantell) to be a freshwater species, a conclusion based upon the stable isotope analyses of Allen and Keith (1965) who measured $\delta^{13}\text{C}$ values of -2‰ . Allen and Keith (1965) also studied *Theriosynoecum allenii* (Pinto and Sanguinetti), for which $\delta^{13}\text{C}$ values of $+0.48\text{‰}$ were quoted. These results, however, were not based upon measurements on the ostracods themselves, but on bivalve fragments from the same bed, which were not necessarily contemporary. These data were, however, used to argue for a wide salinity tolerance for *Theriosynoecum* in general, although Allen *et al.* (1973, p. 615) did concede the potential inaccuracy in the original statement. Tan and Hudson (1974) analysed *Theriosynoecum conopium* Wakefield and Athersuch, 1990, from Bed 7 of the Kilmaluag Formation type section. They found mean $\delta^{13}\text{C}$ of -1.8‰ and mean $\delta^{18}\text{O}$ of -5.9‰ , which they considered to suggest transitional to freshwater environments. Isotopic values for $\delta^{13}\text{C}$ of -0.76‰ and $\delta^{18}\text{O}$ of -2.95‰ , were obtained from a mixed sample of *Theriosynoecum conopium* taken from both Bed 24, Kilmaluag Formation, Camas Mor, Muck, and Bed 3, Kilmaluag Formation, Prince Charles's Point, Skye (J. E. Andrews, pers. comm. 1991). Andrews interprets these results as indicating evaporating 'freshwaters' which were in equilibrium with atmospheric CO_2 . A tolerance of 0–7‰, as given in Kilenyi and Allen (1968), is used in this work.

Salinity tolerance of Linnocythere

Linnocythere is generally regarded as being indicative of fresh waters. Work on Recent species, however, has begun to unravel the hydrochemical controls on the distribution of *Linnocythere*, and has shown that solute chemistry may be more important than absolute salinity. Carbonel and Peypouquet (1979, 1983) and Peypouquet *et al.* (1979) contended that waters lying on the alkaline or continental saline path of Hardie and Eugster (1970) are dominated by *Linnocythere*. However, Martens (1990), in his study of African rift valley species of *Linnocythere*, did not find any convincing evidence that *Linnocythere* prefers alkaline waters. Many records of the salinity tolerance of *Linnocythere* have been taken from continental settings where Na and Cl are not the dominant salts; athalassic environments, which are often alkaline. *Linnocythere staplini* Gutentag and Benson has been recorded living in salinities of up to 205‰ in Australian athalassic waters (DeDecker 1981a). It should be noted that many Australian *Linnocythere* species inhabit much lower salinities, and are generally only found in permanent water bodies (DeDecker 1983), e.g. *Linnocythere milta* (15.4‰, pH 9.5; DeDecker 1981a) and *Linnocythere mowbrayensis* (< 6‰; DeDecker *et al.* 1982). Alkaline waters are created by anionic enrichment and follow an evaporative path through carbonate, bicarbonate and soda. However, the neutral saline path is governed by cationic enrichment and follows an evaporative path through carbonates, sulphates (such as gypsum) and chlorides. There is little doubt that the waters of Lealt Shale environment lay on the neutral saline path. Tan and Hudson (1974, figs 1–2) used stable isotopic analyses of *Praemytilus strathairdensis* to show a direct mixing of seawater and river water, which could be compared with the work of Mook (1971) on mytilids from Dutch estuaries. The Lealt Shale results indicated that the diluting fresh water was richer in ^{13}C than the estuaries studied by Mook (1971). This confirmed the idea that the Lealt Shale was deposited in lagoons with a direct link to marine waters which controlled variations in salinity. Hudson (1970) recorded pseudomorphs after gypsum in the algal stromatolitic limestone at the top of the Kildonnan Member. This again adds weight to the argument that the Lealt Shale waters were of a neutral saline chemistry, and that salinity tolerances from species inhabiting alkaline waters may not be applicable in this instance. Forester (1983) was able to show that *Linnocythere* inhabiting lacustrine environments were governed by



TEXT-FIG. 5. Percentage composition of the ostracod fauna containing only *Linnocythere incerniculum* (solid line) and *Darwinula pulmo* (unshaded line), from the Kildonnann Member at Rudha nam Braithairean/Brothers Point, Skye.

solute chemistry rather than by salinity. Again, although of interest, this factor may not be applicable to the Lealt Shale waters as he was studying inland lakes.

Würdig (1983) recorded *Linnocythere* sp. A at salinities of 0–2‰ in the coastal lagoons of eastern Brazil. Wagner (1957) recorded *Linnocythere inopinata* in waters of low salinity (< 3‰). However, Neale (1988) gives the species a tolerance range of 0–33‰ with a preference for salinities below 13‰. Lealt Shale species of *Linnocythere* often occur *in situ* with other freshwater ostracods such as *Theriosynoecium* and *Darwinula* (see discussion above and below). However, the *Linnocythere* species also occur in assemblages where they are *in situ* with genera considered to be tolerant of higher salinities, and with *Darwinula* and *Theriosynoecium* absent. Co-occurrences with *Praemytilus strathairdensis* indicate that the Kildonnann *Linnocythere* species could tolerate mesohaline salinities. Based on this evidence it is considered that *Linnocythere* had a tolerance range from freshwater into mesohaline salinities, but probably not into polyhaline waters. The range, therefore, is considered for the purposes of this work, to be approximately 0–15‰, although as the discussion above illustrates, *Linnocythere* occurrence is governed by a wide range of chemical

controls, of which salinity is only one. The salinity range given here, when compared with the molluscan fauna with which *Linnocythere* occurs, appears to be plausible, although the range is considered only to be semi-quantitative.

Salinity tolerance of Darwinula

The salinity tolerance of *Darwinula* can also be based upon studies of Recent species, e.g. *Darwinula stevensoni*. Neale (1988) indicates a tolerance of 0–15‰ for *Darwinula stevensoni*, but notes that it is found at its maximum abundance in salinities of 0–2‰. Hagerman (1967) found that *Darwinula stevensoni* was at its maximum abundance in waters of 3‰ in the Gulf of Finland. This indicates that *Darwinula stevensoni* has a preference for waters of very low salinity. An upper salinity tolerance limit is based upon observations of *Darwinula* in some inland lakes of Australia, where it has been found in salinities of up to 15‰ (Keyser 1977; DeDeckker 1981a). This implies that at very low salinities *Linnocythere* and *Darwinula* are likely to coexist. However, at higher salinities (5–15‰) *Linnocythere* may begin to dominate numerically the assemblage as *Darwinula* approaches its maximum tolerance. This type of association was noted at many levels in the Lealt Shale Formation but particularly in the Kildonnan Member at Rudha nam Braithairean (Text-fig. 5). Here *Linnocythere incerniculum* comprises some 88–93 per cent. of the ostracod fauna, *Darwinula pulmo* being the only other ostracod present in the samples studied. These assemblages have been determined to be autochthonous. Gramann (1971) suggested that some Triassic *Darwinula* species may have had a wider salinity tolerance than Recent species. This conclusion was based upon the association of *Darwinula* with deposits interpreted as having formed in a hypersaline environment. Kilenyi and Neale (1978) felt that these *Darwinula* specimens had not coexisted with the hypersaline conditions; rather they had been killed as the increasing salinity passed their upper tolerance limit, and were then incorporated *in situ* into the evaporites. Other evidence as to the generally low salinities inhabited by Recent species of *Darwinula*, other than *Darwinula stevensoni*, was given by Würdig (1983), in which the following tolerances were given; *Darwinula serricaudata espinosa* Pinto and Kotzian, 1961 (0–3‰); *Darwinula pagliolii* Pinto and Kotzian, 1961 (0–3‰); *Darwinula africana brasiliensis* Pinto and Kotzian, 1961 (0–3‰) and *Darwinula* sp. A Würdig, 1983 (0–11‰).

A salinity tolerance of 0–15‰ with a preference for lower salinities in the oligohaline range, 0–5‰, is used in this work.

Salinity tolerances of the Ostracoda from the Kildonnan Member

Darwinula pulmo was found to occur almost exclusively with *Linnocythere incerniculum*, but often constituted only a small component of the assemblage. In most associations with only these two species, *Linnocythere incerniculum* comprised 90 per cent. of the assemblage. This was particularly evident in the Kildonnan Member sampled at Rudha nam Braithairean (Text-fig. 5). This finding is consistent with the assumed relative salinity tolerances used. *Linnocythere incerniculum* is considered to have tolerated a wider range of salinities (0–15‰) than *Darwinula pulmo* (0–10‰ with a preference for 0–5‰).

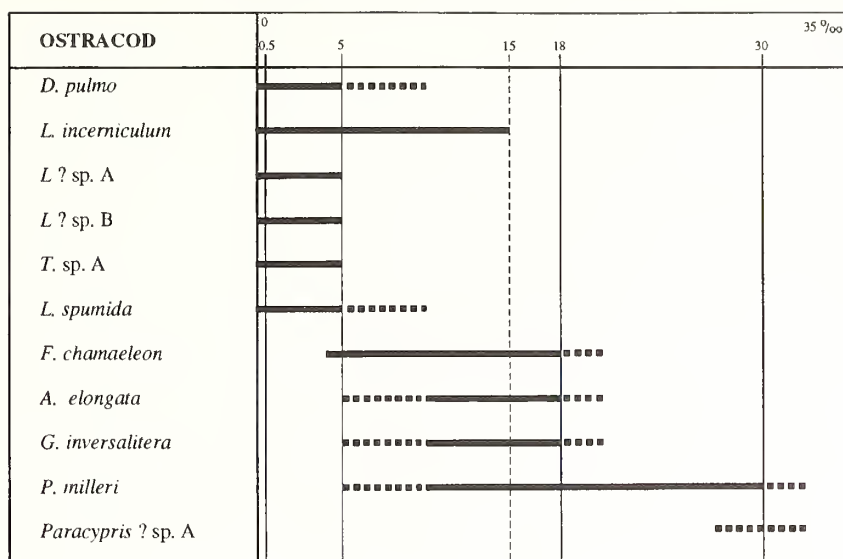
Linnocythere? sp. A (one valve), *Linnocythere?* sp. B (two valves) and *Theriosynoecum* sp. A (one valve) were not found in numbers that suggested that they were *in situ*. All were, however, found in association with *Linnocythere incerniculum* and *Darwinula pulmo*, when these latter two species were not considered to be *in situ*. By association, therefore, *Linnocythere?* sp. A, *Linnocythere?* sp. B and *Theriosynoecum* sp. A are tentatively considered to have lived in fresh and oligohaline waters (0–5‰).

Linnocythere spunida is also considered to have preferred fresh to oligohaline salinities (0–5‰), but like *Darwinula pulmo* may have tolerated slightly higher salinities. This conclusion is based upon assemblages of *Linnocythere incerniculum* with small but approximately equal numbers of *Darwinula pulmo* and *Linnocythere spunida*. *Linnocythere spunida* was not found *in situ* in any population dominated by the euryhaline marine ostracods defined below, e.g. *Glyptocythere inversalitera*.

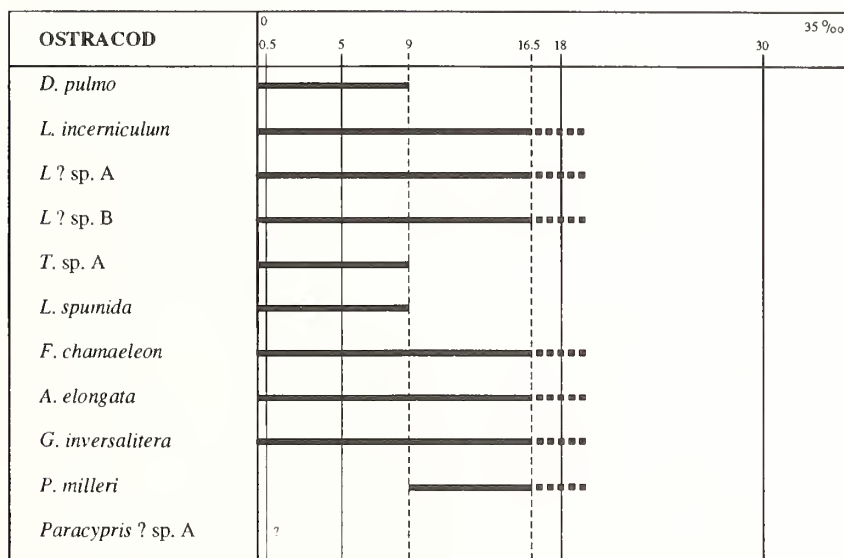
Fronslarvata chamaeleon is considered to have been tolerant of mesohaline salinities. This is also the case for *Acanthocythere elongata* and *Glyptocythere inversalitera*. Two of these species are often found in association, but never all at the same time, as their stratigraphical ranges do not overlap (Wakefield 1994, fig. 46). Their lower salinity tolerance limits are, however, considered to have been slightly different. *Acanthocythere elongata* and *Glyptocythere inversalitera* do not appear to have tolerated quite such low salinities as *Fronslarvata chamaeleon*. All three species have been found in association with *Linnocythere incerniculum*, which was considered to have been *in situ* but probably towards the upper limit of its salinity tolerance (15‰). In Bed 4a of the Kildonnan Member type section *Glyptocythere inversalitera* comprises 56 per cent., *Fronslarvata chamaeleon* 21 per cent. and *Linnocythere incerniculum* 20 per cent. of the assemblage. *Linnocythere?* sp. A and *Linnocythere spinida* complete the association (3 per cent.). In the middle of Bed 5e (same locality), the assemblage is composed of *Linnocythere incerniculum* (26 per cent.), *Fronslarvata chamaeleon* (31 per cent.) and *Acanthocythere elongata* (31 per cent.), with *Linnocythere spinida* and *Darwinula pulmo* (8 per cent. and 4 per cent. respectively) not considered to be *in situ*. At the top of Bed 5f (same locality) *Fronslarvata chamaeleon* comprises 49 per cent. and *Acanthocythere elongata* 46 per cent. of the assemblage with *Darwinula pulmo* (5 per cent.) not considered to be *in situ*. Evidence for a lower salinity tolerance of *Fronslarvata chamaeleon* was noted in a sample from the lower half of Bed 5e (same locality) where *Acanthocythere elongata* (3 per cent.) is not considered to be *in situ*, while *Fronslarvata chamaeleon* (51 per cent.) and *Linnocythere incerniculum* (31 per cent.) are considered to be *in situ*. In beds where *Glyptocythere inversalitera* dominates, *Fronslarvata chamaeleon* is generally subordinate. Therefore, *Fronslarvata chamaeleon* is considered to have tolerated salinities as low as 5–10‰, whereas *Acanthocythere elongata* and *Glyptocythere inversalitera* tolerated salinities only slightly below 15‰. *Acanthocythere* and *Glyptocythere* have generally been considered to be indicative of marine conditions, e.g. Morkhoven (1963), Bate (1967), Ware and Whatley (1980, 1983) and Harten and Hinte (1984). However, evidence is now appearing for the general euryhalinity of some species of *Glyptocythere*. Both Stephens (1980) and Sheppard (1981) considered *Glyptocythere guembeliana* (Jones) and *Glyptocythere penni* Bate and Mayes to have tolerated low brackish salinities, but not to have coexisted with *Darwinula* and *Theriosynoecum*. A lower limit of 10‰, therefore, seems reasonable. The upper salinity limit of the three species is more difficult to determine. All three occur in populations where *Linnocythere incerniculum* is not considered to be *in situ* or is absent. This indicates a tolerance above 15‰. In some samples *Glyptocythere inversalitera* dominates over *Fronslarvata chamaeleon* as does *Acanthocythere elongata*, suggesting that *Fronslarvata chamaeleon* did not tolerate as high a salinity as the other two genera. It is not possible on the ostracod evidence alone to determine an upper salinity limit. The fact that neither *Glyptocythere inversalitera* nor *Acanthocythere elongata* are found in assemblages which, by their generic composition, are most likely to have been marine, e.g. with *Lophocythere*, *Looneyella*, *Fastigatocythere*, *Paracypris*, *Pichottia*, *Schuleridea*, may suggest that the highest salinities that they could tolerate were in the polyhaline range (18–30‰).

Both *Progonocythere* and *Paracypris* are generally considered to be marine genera (Bate 1967; Neale 1988). However, in Bed 6, Kildonnan Member, North Shore, Eigg, *Progonocythere milleri* is found in association with *Linnocythere incerniculum*. Although *Linnocythere incerniculum* dominates the assemblage, 81 per cent., as compared with 19 per cent. for *Progonocythere milleri*, male, female and three juvenile stages of *Progonocythere milleri* were present indicating that it was *in situ* and probably able to tolerate salinities lower than 15‰. No samples were found where *Progonocythere milleri* was considered to have co-occurred *in situ* with *Darwinula pulmo*, indicating that the lower limit of its tolerance range was not below 10‰. *Paracypris?* sp. A was never found *in situ*, suggesting that its generic salinity tolerance range was never reached in the exposed parts of Kildonnan Member. The fact that it does not occur *in situ* with *Glyptocythere inversalitera* or *Acanthocythere elongata* confirms the suggestion that it tolerated salinities that were in all probability 30‰ and higher, and that they, in turn, tolerated salinities lower than 30‰.

A chart of the different relative salinity tolerances for the Ostracoda from the Kildonnan Member is given in Text-figure 6. In order to test these salinity tolerances, considering that they were



TEXT-FIG. 6. Inferred relative salinity tolerances of the Kildonnann Member Ostracoda based upon co-occurrences with other ostracods. Solid line indicates preferred salinity tolerance range; dashed line indicates possible further limits of tolerance range.



TEXT-FIG. 7. Inferred relative salinity tolerances of the Kildonnann Member Ostracoda based upon co-occurrences with the mollusc and conchostracan fauna. Solid line indicates preferred salinity tolerance range; dashed line indicates possible further limits of tolerance range.

based upon several assumptions, a similar chart was constructed using the ostracods *in situ* association with the molluscan and conchostracan fauna. The salinity tolerances for the mollusc and conchostracan fauna are those of Hudson (1963a). A comparison of this chart (Text-fig. 7)

with Text-figure 6 indicates a broad similarity of estimated tolerances. Therefore, the relative salinity tolerances of the Ostracoda from the Kildonnan Member are considered to be valid.

Salinity tolerances of the Ostracoda from the Lonfearn Member

Linnocythere spinosa and *Darwinula phaselus* are usually found in association. As with *Linnocythere incerniculum* and *Darwinula pulmo* in the Kildonnan Member, *Linnocythere spinosa* generally dominated the association, e.g. in Bed 3 of the Lonfearn Member at Rudha nam Braithairean. *Linnocythere spinosa* comprises 89–98 per cent. of the ostracod fauna, *Darwinula phaselus* being the only other ostracod present in the samples. Thus, *Linnocythere spinosa* is considered to have tolerated slightly higher salinities than *Darwinula phaselus*; 0–15‰ and 0–10‰ respectively. These tolerances are the same as those given for *Linnocythere incerniculum* and *Darwinula pulmo* respectively. It is not possible to test this similarity as no ostracod occurs in both members of the Lealt Shale Formation. The fact that the bivalve *Neomiodon brycei* occurs with all four species indicates a close similarity of salinity tolerances or overlap of tolerance ranges.

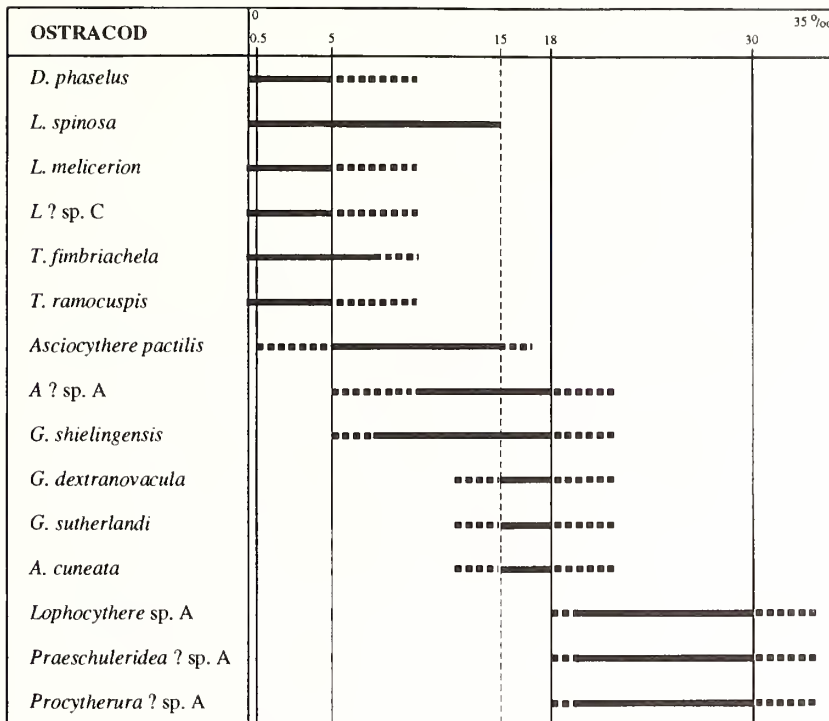
Linnocythere melicerion, *Linnocythere?* sp. C and *Theriosynoecium fimbriachela* occur *in situ* with *Linnocythere spinosa* and *Darwinula phaselus*, which is consistent with the assumed salinity tolerances of species of these genera.

Theriosynoecium ramocuspis has not been recorded *in situ* with any other Lonfearn Member ostracods. Its salinity tolerance, therefore, is taken to be that preferred by the genus, 0–7‰.

Glyptocythere shielingensis was found in some samples to be *in situ* with *Theriosynoecium fimbriachela*, e.g. in Bed 11 of the Lonfearn Member from the Shieling Burn section. Adults and at least three juvenile stages of *Glyptocythere shielingensis* and adults with four juvenile stages of *Theriosynoecium fimbriachela* were recorded in a sample from this bed, indicating that *Glyptocythere shielingensis* could tolerate very low salinities, maybe as low as 5‰. No evidence for faunal mixing has been documented for this horizon. It is not possible to determine an upper salinity tolerance for this species, but the euryhaline nature of *Glyptocythere* suggests that its overall tolerance range may have been large. As previously noted (Stephens 1980; Sheppard 1981), *Glyptocythere* is considered to be highly euryhaline but, until this occurrence, had not been found *in situ* with *Theriosynoecium*. This occurrence may be explained by the findings of Forester and Brouwers (1985), who noted that marine ostracods from Na- and Cl-dominated waters, could survive in fresh waters also dominated by Na and Cl. This may be the case for Lealt Shale waters with their direct sea water/fresh water mixing (Tan and Hudson 1974).

Glyptocythere dextranovacula, *Glyptocythere sutherlandi*, *Aalenella cuneata* and *Lophocythere* sp. A generally occur in the same samples. *Glyptocythere dextranovacula* and *Glyptocythere sutherlandi* were used in Wakefield (1991, 1994) to indicate the base of the Lonfearn Member. The association indicates similar salinity tolerances. *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi* and *Aalenella cuneata* do not co-occur *in situ* with *Linnocythere spinosa*, indicating a salinity tolerance above 15‰. *Lophocythere* sp. A is never found in large numbers and no adults have been recovered from the samples studied. *Lophocythere* is generally considered to be indicative of marine conditions (Morkhoven 1963; Stephens 1980; Sheppard 1981; Harten and Hinte 1984). These two factors lead to the conclusion that *Lophocythere* sp. A did not tolerate such low salinities as *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi* or *Aalenella cuneata*. Although the evidence is not substantial, the lack of association with a demonstrably marine fauna indicates that *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi* and *Aalenella cuneata* tolerated salinities in the order of 15–30‰. *Lophocythere* sp. A probably preferred salinities in the upper portion of this range through to fully marine conditions, but this is conjectural. It is reasonably safe to say that fully marine conditions were not experienced in the sections sampled.

Asciocythere pactilis co-occurs *in situ* with: (a) *Linnocythere spinosa* and *Darwinula phaselus* in one association (e.g. top of Bed 3 and base of Bed 5, Lonfearn Member, Rudha nam Braithairean, Skye); and (b) *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi* and *Aalenella cuneata* in



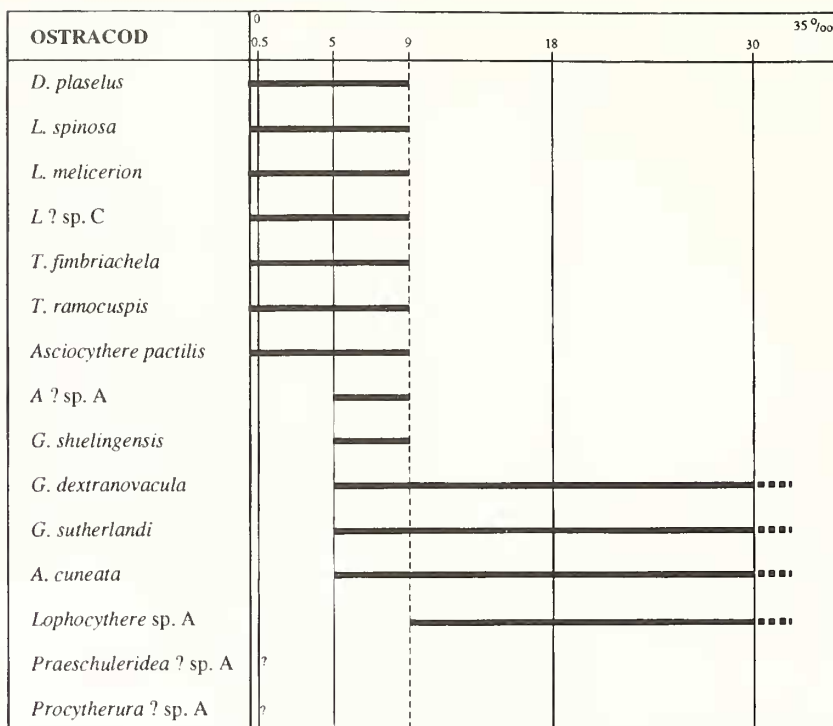
TEXT-FIG. 8. Inferred relative salinity tolerances of the Lofearn Member Ostracoda based upon co-occurrences with other ostracods. Solid line indicates preferred salinity tolerance range, dashed line possible further limits of tolerance range.

another (e.g. top of Bed 1, Lofearn Member, Rudha nam Braithairean, Skye). *Asciothyre pacilis*, therefore, would appear to be either highly euryhaline, or to tolerate a narrow salinity band which bridges the gap between the salinity tolerances of the two associations. In the sample from the top of Bed 3, Lofearn Member, Rudha nam Braithairean, *Asciothyre pacilis* constitutes 58 per cent. of the ostracods present, *Limnocythere spinosa* 35 per cent., *Darwinula phaselus* 7 per cent. along with a single valve of *Praeschuleridea ? sp. A* Wakefield, 1994. Males, females and five juvenile stages are preserved of *Asciothyre pacilis* indicating its autochthoneity. This association indicates a tolerance by *Asciothyre pacilis* of salinities higher than those of waters usually inhabited by *Darwinula phaselus*; greater than 5‰. In its association with the higher salinity group *Asciothyre pacilis* occurs in small numbers. A tolerance range of 5–18‰ is used in this work.

Acauthocythere ? sp. A occurs as a minor constituent of assemblages including *Limnocythere spinosa*, *Darwinula phaselus* and *Limnocythere melicerion* indicating a potential tolerance below 10‰, and perhaps as low as 5‰. It is not possible to determine the upper salinity tolerance limit. This may be similar to that of *Acauthocythere elongata* from the Kildonnan Member.

Praeschuleridea ? sp. A and *Procytherura ? sp. A* occur in small numbers; two valves for each species. Both genera have been found in marine associations (Bate 1967; Ware and Whatley 1980, 1983).

A chart of the relative salinity tolerances of the Ostracoda from the Lofearn Member is given in Text-figure 8. As with the Kildonnan Member this chart can be compared with one drawn up using *in situ* species co-occurrences with the mollusc and conchostracan fauna (Text-fig. 9).



TEXT-FIG. 9. Inferred relative salinity tolerances of the Lonfearn Member Ostracoda based upon co-occurrences with the mollusc and conchostracan fauna. Solid line indicates preferred salinity tolerance range, dashed line possible further limits of tolerance range.

PALAEOSALINITY FLUCTUATIONS IN THE LEALT SHALE FORMATION

Previous interpretations have noted numerous palaeosalinity fluctuations within the Lealt Shale Formation (Hudson 1963*a*, 1966; Hudson and Harris 1979; Walton 1988; Riding *et al.* 1991). It was, therefore, decided to compare the palaeosalinity curves defined by the different faunas present within the Lealt Shale Formation. Palaeosalinity curves were constructed not just for the type section of the Kildonnan Member but also for the Kildonnan and Lonfearn members at Rudha nam Braithairean, Skye and North Shore, Eigg as well as for the Lonfearn Member at Sheiling Burn, Eigg. Few samples were available for study from the last two sections. However, the ostracod occurrences in these two sections proved invaluable in reconstructing the relative salinity tolerances of the ostracods. The Kildonnan and Lonfearn sections exposed immediately north of Elgol, Strathaird, Skye were not included in this study because of the extremely poor record of ostracods from those sections.

The first palaeosalinity curve constructed for each section used the mollusc and conchostracan fauna noted in the samples taken for the ostracod studies. The salinity tolerances suggested for the molluscs and conchostracans by Hudson (1963*a*) and Hudson and Harris (1979) were used. The second palaeosalinity reconstruction uses the ostracod salinity tolerances defined above. When an ostracod species dominated a sample with respect to another, the salinity was taken to be on the dominant species side of their tolerance range overlap. Although this is a logical step to take it need not necessarily represent what actually occurred, but is a best estimate. The size of the error bars produced by the above methods, and the gaps between sample positions, serve to obscure the exact shape of the palaeosalinity curve. The gaps between samples may hold a far more complicated salinity history than that implied by the tie lines, which only indicate a general trend. For the type

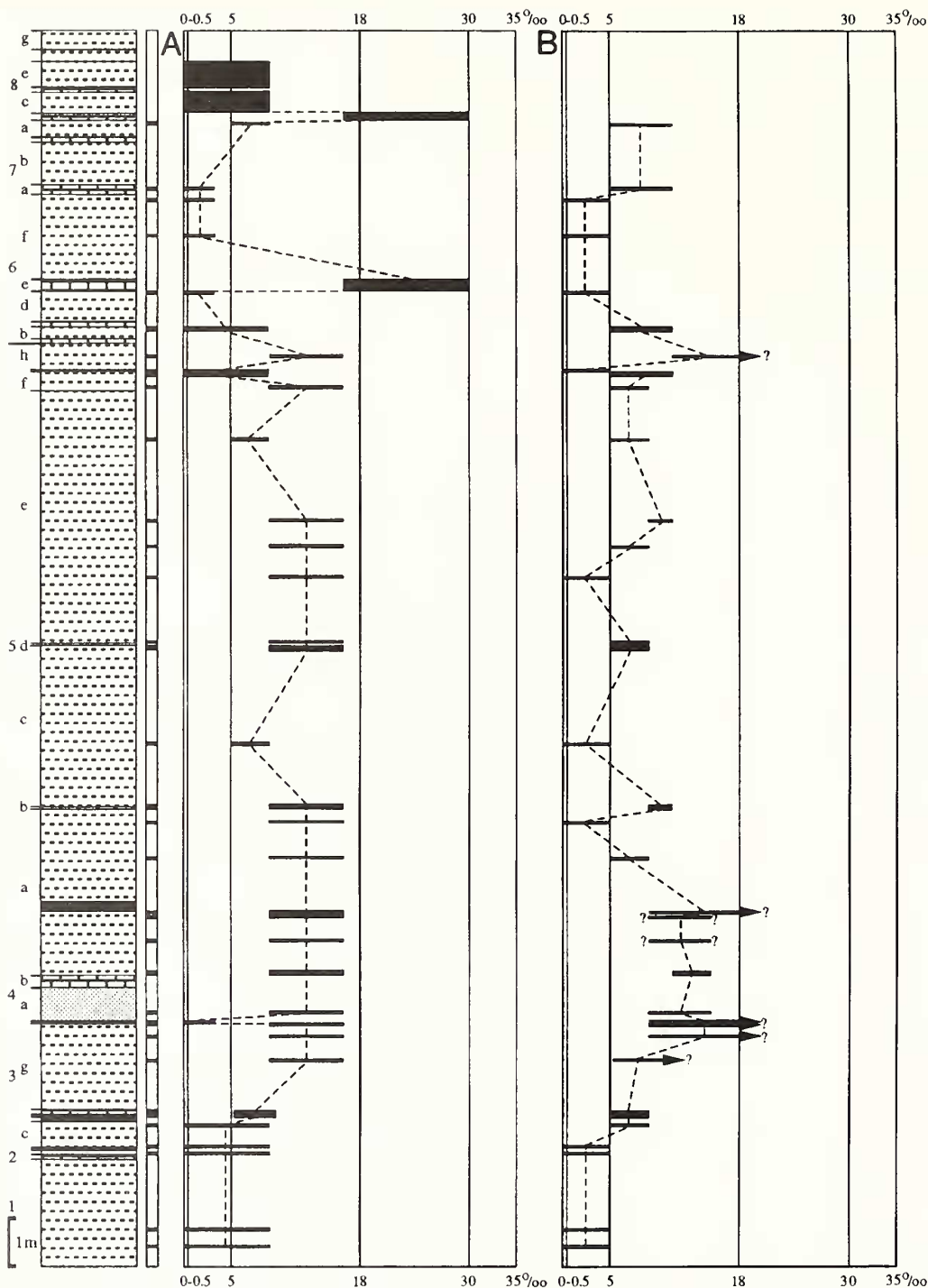
section of the Kildonnan Member and the Rudha nam Braithairean sections a plot is given of the percentage abundances of *Botryococcus* with respect to the total palynoflora; this data is taken from Walton (1988). *Botryococcus* is a fresh to brackish water planktic member of the Chlorophyceae (green algae), high percentages of which can be equated with fresh to brackish waters (Naumann 1922; Hutchison 1957). Finally, an attempt was made to reconstruct a palaeosalinity envelope for the type section of the Kildonnan Member and the Rudha nam Braithairean section using all of the data available.

Palaeosalinity curve for the Kildonnan Member type section

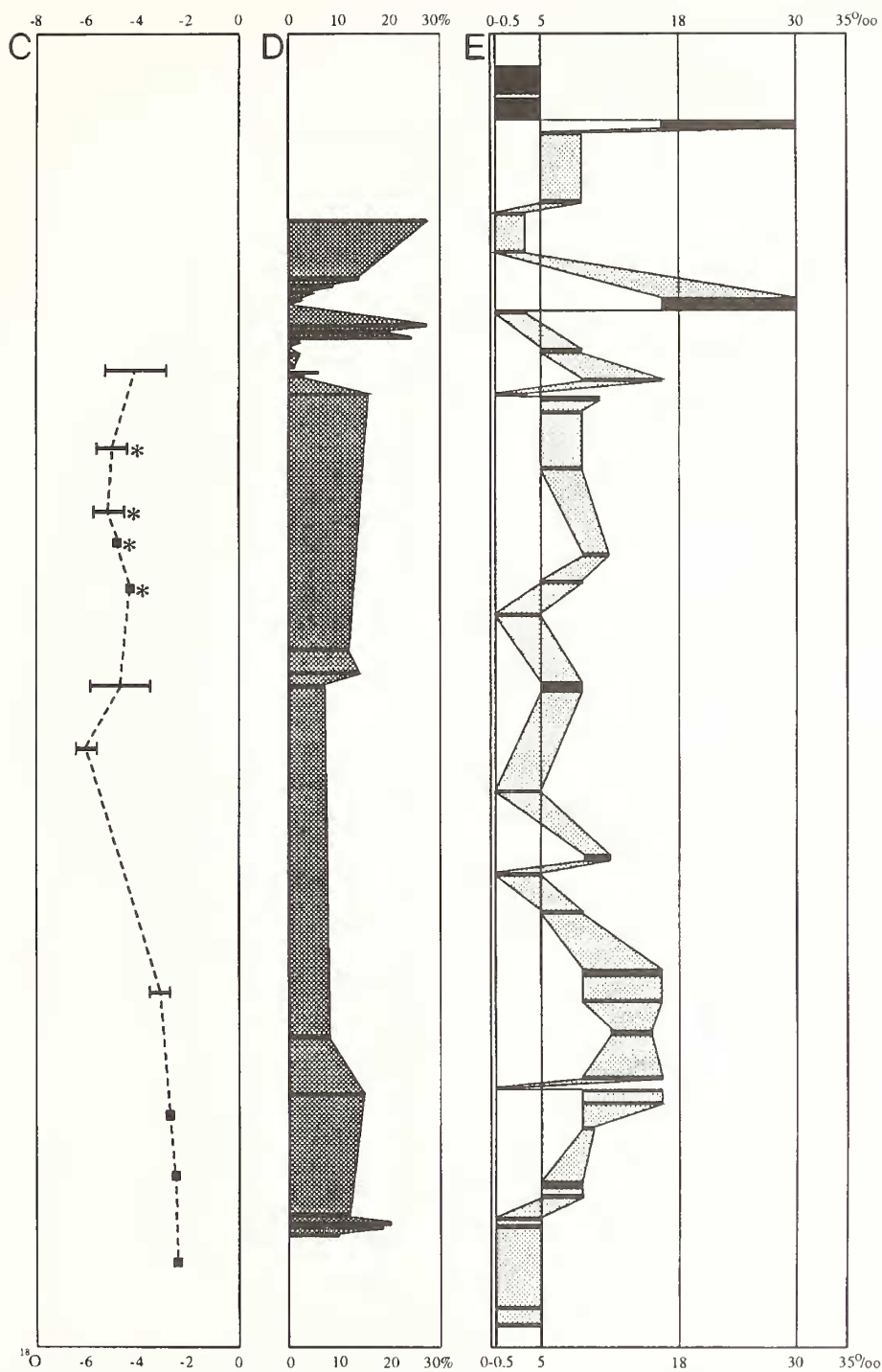
The palaeosalinity curve derived from the molluscs and conchostracans (Text-fig. 10A) in general mirrors that derived from the ostracod fauna (Text-fig. 10B), although there are several subtle differences between the two. These were to be expected considering the differences in the number of species available for each study, which in turn produces differences in the coarseness of the relative salinity tolerances within each group. The ostracods appear, however, in most instances, to allow a more accurate palaeosalinity curve to be defined than is possible using the mollusc and conchostracan fauna.

Both Beds 1 and 3a were deposited under fresh to oligohaline salinities (0–5‰). The faunas of both beds are dominated by the ostracods *Linnocythere incerniculum* and *Darwinula pulmo*, conchostracans, the gastropods *Viviparus scoticus* and *Valvata* sp., as well as fish fragments. An increase in salinity at the top of Bed 3c is indicated by the presence of the ostracods *Fronsarvata chamaeleon* and *Linnocythere incerniculum*, which are accompanied in Beds 3e and 3f by small specimens of the bivalve *Praemytilus strathairdensis*. This salinity increase continues into Beds 3g and 3h, where the ostracods *Fronsarvata chamaeleon* and *Glyptocythere inversalitera*, and the bivalve *Praemytilus strathairdensis* dominate. Salinities were probably around 18‰ but may have been higher. The middle of Bed 3g contains large numbers of fish otoliths as does the base of Bed 5e. Similar concentrations are known from the Oxford Clay and are referred to as coprocoenoses. Otoliths are coated by a thick organic membrane which allows them to pass through the intestines of fish, unlike the other skeletal bones. Otoliths are, therefore, likely to be concentrated preferentially (D. M. Martill, pers. comm. 1991). Some otoliths from Bed 3g were analysed using an X-ray diffractometer by Mr R. N. Wilson (Leicester University), and proved to be composed of the unaltered original aragonite. At present some specimens of these otoliths from Bed 3g are being analysed isotopically (C and O) by T. F. Anderson. It is hoped that this work will increase the information available on water chemistry and probably salinity. Although the *Fronsarvata chamaeleon*, *Glyptocythere inversalitera*, *Praemytilus strathairdensis* fauna is present at the top of Bed 3h, the *Praemytilus strathairdensis* valves are fragmentary, whilst large undamaged specimens of the bivalve *Unio andersoni* (up to 60 mm in length) are present. The undamaged specimens of *Unio andersoni* indicate salinities that were at their highest oligohaline; lower than those estimated for *Praemytilus strathairdensis*. The lower part of Bed 3h is silty and contains thin plasters of *Praemytilus strathairdensis* with *Fronsarvata chamaeleon* and *Glyptocythere inversalitera* visible on the laminations. The upper 10–20 mm of the bed is a *Praemytilus* shell hash, indicating strong current winnowing. Large amounts of phosphatic fish bones and teeth are present as well as specimens of *Fronsarvata chamaeleon* which are difficult to detect amongst the shell hash. It appears that *Unio andersoni* inhabited the shell hash after its deposition and a subsequent reduction in salinity to 0–3‰. *Darwinula pulmo* and *Linnocythere incerniculum* were more obvious and numerous in the shell hash than in the lower portion of the bed. However, the shell hash also contains large numbers of reworked (but most probably indigenous) *Fronsarvata chamaeleon* and *Glyptocythere inversalitera*, which essentially dilute the palaeoenvironmental signature of *Darwinula* and *Linnocythere* when counts of the ostracods are taken. The occurrence, in Bed 3h, of brackish water tolerant palynomorphs corroborates these findings (Walton 1988).

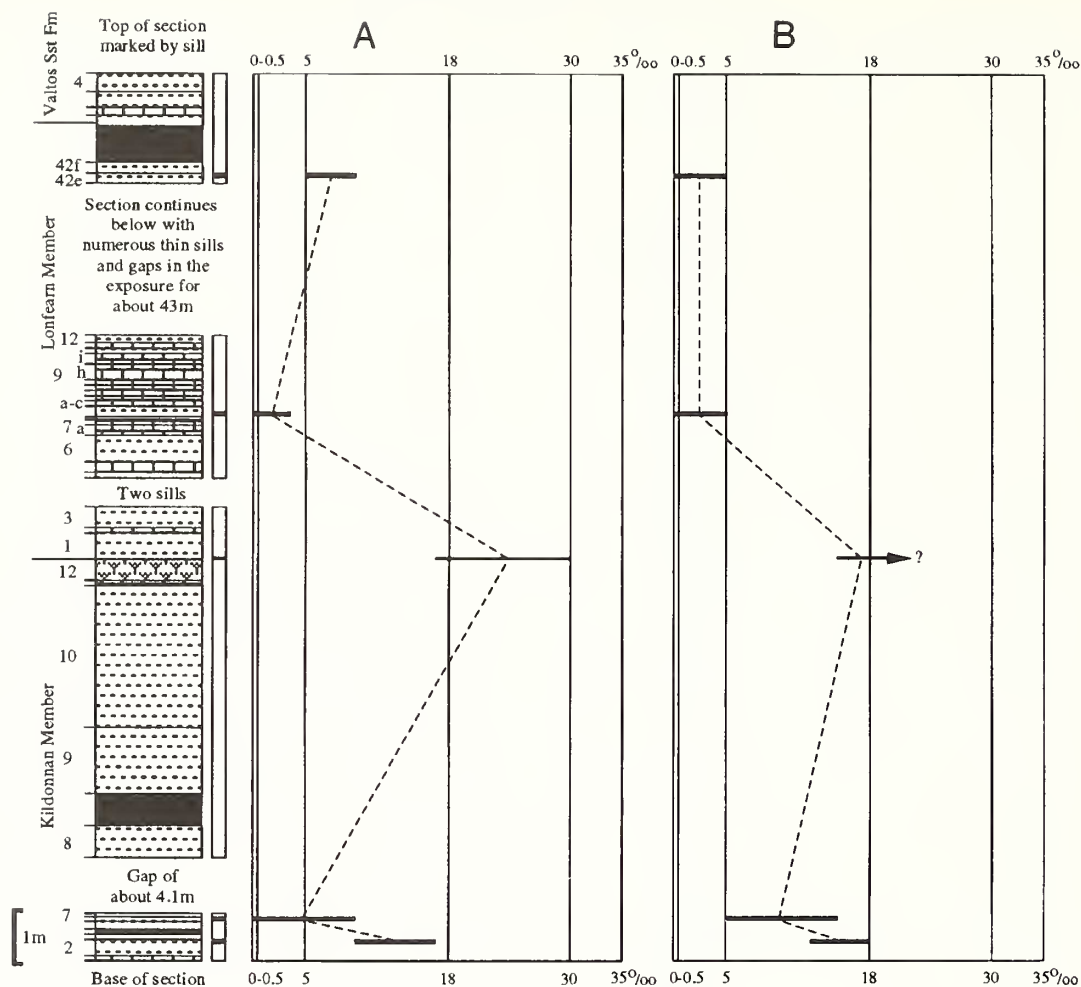
A shale intercalation within the essentially sandy Complex Bed (Bed 4) contains a brackish water fauna composed of the ostracods *Linnocythere incerniculum*, *Fronsarvata chamaeleon*,



TEXT-FIG. 10. Kildonnan Member, Lealt Shale Formation, type section, Eigg. A, palaeosalinity curve defined using mollusc and conchostracan assemblages; salinity values of the fauna based upon Hudson (1963a). B, palaeosalinity curve defined using ostracod assemblages. C, $\delta^{18}\text{O}$ values from *Praemytilus strathairdensis*;



approximate positions of samples analysed are shown; those marked * were only approximately positioned in the original paper; data from Tan and Hudson (1974). D, *Botryococcus* abundances expressed as a percentage of the total palynoflora; approximate positions of samples are shown; data from Walton (1988). E, composite palaeosalinity curve based on all data.

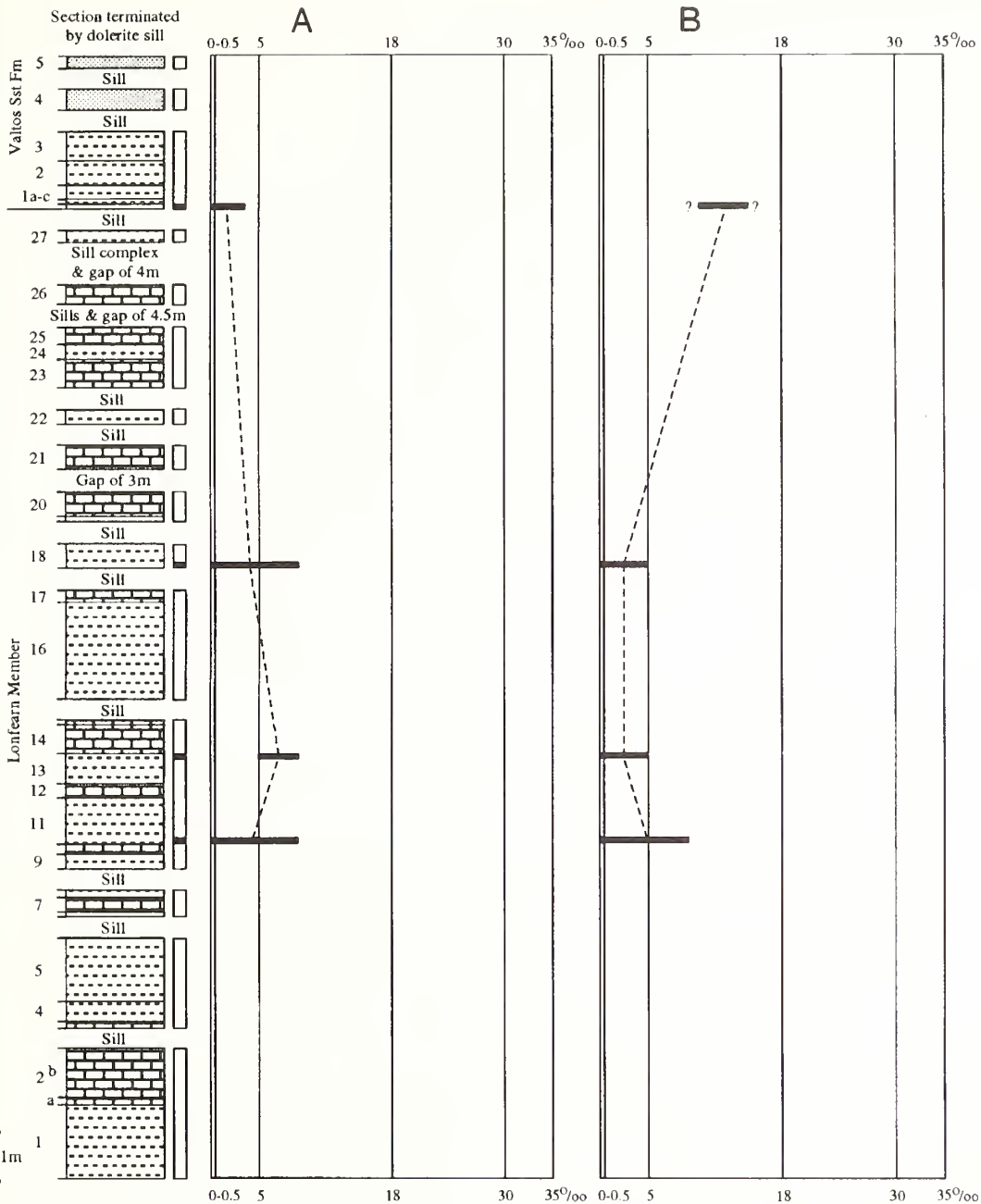


TEXT-FIG. 11. Kildonnan and Lonfean Members, North Shore, Eigg. A, palaeosalinity curve defined using mollusc and conchostracan assemblages; salinity values based upon Hudson (1963a). B, palaeosalinity curve defined using ostracod assemblages.

Glyptocythere inversalitera and the bivalve *Praemytilus strathairdensis*. Salinities were probably around 15‰.

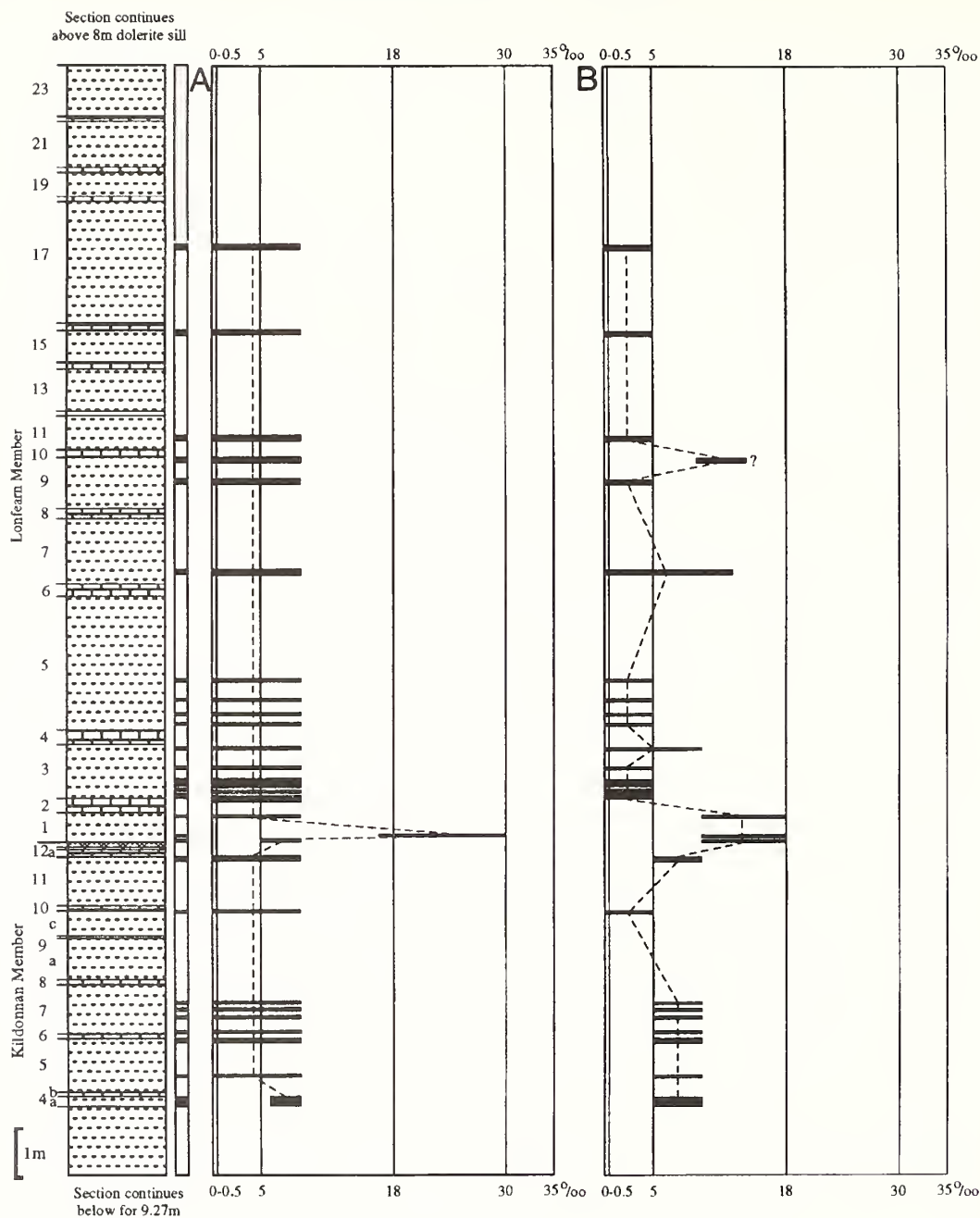
Bed 5, as a whole, has a highly fluctuating palaeosalinity. The mollusc fauna was dominated by the bivalve *Praemytilus strathairdensis*, though the gastropod *Valvata* sp. was occasionally present. It is not possible using this mollusc fauna to distinguish the salinity fluctuations revealed by the ostracod-derived curve as the generally wide salinity tolerance of *Praemytilus strathairdensis* (10‰ to above 20‰) obscures the subtle changes. A strong positive correlation between the palaeosalinity curve defined using the ostracods (Text-fig. 10B) and $\delta^{18}\text{O}$ values of the bivalve *Praemytilus strathairdensis* (Text-fig. 10C) taken from Tan and Hudson (1974) was observed. Generally 'heavier' oxygen values correlate with higher salinities and 'lighter' values correlate with lower salinities.

Bed 6 records a gradual decrease in salinity with the ostracods *Linnocythere incerniculum* and *Darwinula pulmo* becoming dominant. Walton (1988) noted 'marine' influences, based on the palynomorph flora, in Beds 6b, 6c, the base of 6d, 6e and at the base of 6f. Of these beds only 6b



TEXT-FIG. 12. Longfearn Member, Shieling Burn, Eigg. A, palaeosalinity curve defined using mollusc and conchostracan assemblages; salinity values based upon Hudson (1963a). B, palaeosalinity curve defined using ostracod assemblages.

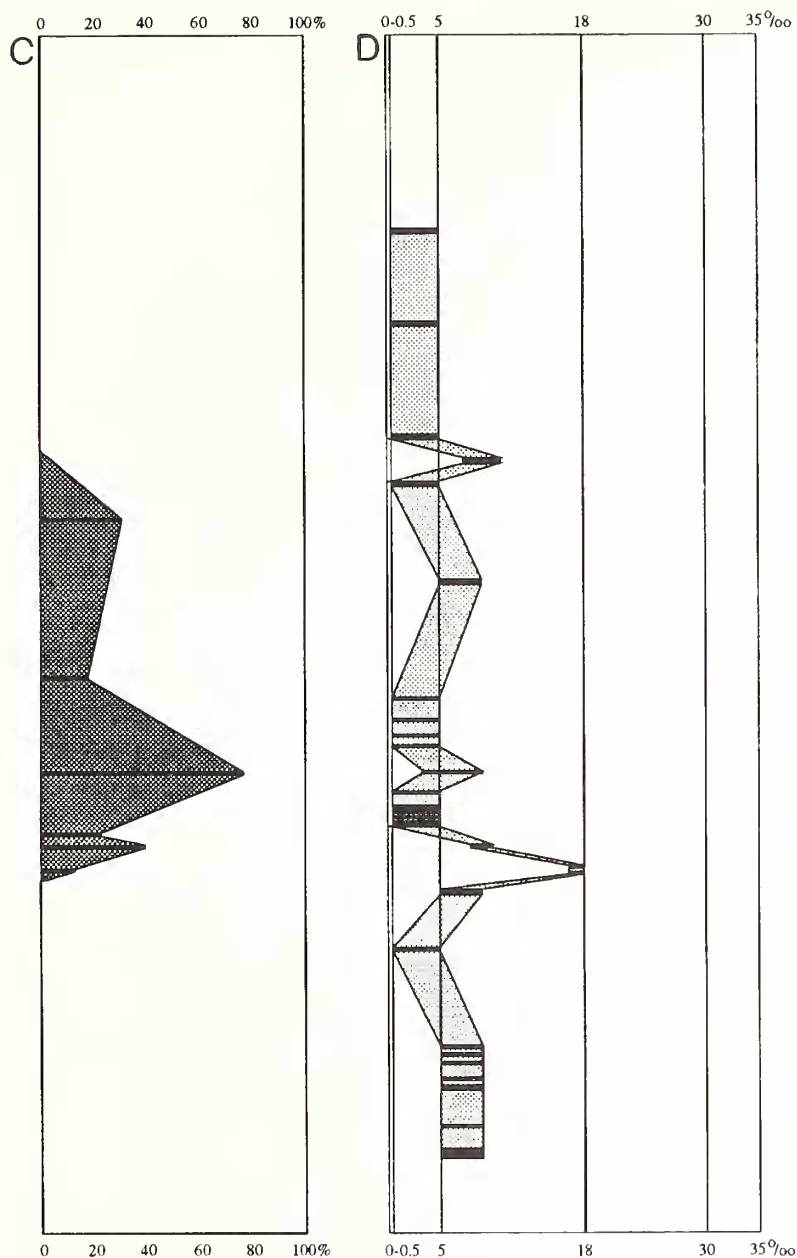
was sampled in this study in the same position as the palynomorph sample site, for which a salinity of around 10‰ is estimated. The *Botryococcus* data (Text-fig. 10D) shows these 'marine' episodes clearly. A negative correlation between palaeosalinity and *Botryococcus* abundances was observed.



TEXT-FIG. 13A-B. For caption see opposite.

Freshwater/oligohaline conditions became fully established in the *Unio* Bed (Bed 7a) where the bivalve *Unio andersoni* occurs with the ostracods *Limnocythere incerniculum* and *Darwinula pulmo*.

A slight rise in salinity is inferred in Bed 8a where *Limnocythere incerniculum* dominates the ostracod fauna over *Darwinula pulmo*. The salinity was probably in the order of 5–10‰. The occurrence of *Neoniodon brycei* as the dominant bivalve is consistent with this conclusion. Bed 8b



TEXT-FIG. 13. Kildonnan and Lonfearn Members, Rudha nam Braithairean, Skye. A, palaeosalinity curve defined using mollusc and conchostracan assemblages; salinity values based upon Hudson (1963a). B, palaeosalinity curve defined using ostracod assemblages. C, *Botryococcus* abundances expressed as a percentage of the total palynoflora; approximate positions of samples are shown; data from Walton (1988). D, composite palaeosalinity curve based on all data.

contains specimens of the bivalve *Placunopsis socialis*, which is indicative of mesohaline salinities. A return to salinities of around 5‰ is indicated in Beds 8d–g by the occurrence of *Neomiodon brycei* and conchostracans, prior to a rise in salinity before the establishment of stromatolitic

cyanobacterial mats, which cannot be documented in detail at the type section (Harris and Hudson 1980).

Palaeosalinity curve for the Kildonnan and Lonfearn Members, North-Shore, Eigg

Very few samples taken from this section, when processed, yielded any ostracods. This was probably a result of metamorphism by the numerous thin sills and dykes intruded into the sediments.

The palaeosalinity curves calculated for the section are given in Text-figure 11A–B. One notable addition to the story of the Lealt Shale Formation is the high salinity fauna recorded from immediately above the Algal Bed. This fauna included the ostracods *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi*, *Aalenella cmeata* and *Lophocythere* sp. A as well as the bivalve genera *Placumopsis* and *Cuspidaria*. The estimated palaeosalinity is at least 20‰, but probably was somewhat higher. The lack of large numbers of the ostracod *Lophocythere* sp. A indicates that the salinity probably did not reach 30–35‰ (see comments in Rudha nam Braithairean subsection about the significance of the ostracod *Progonocythere milleri* recovered from Bed 7 of the Kildonnan Member).

Palaeosalinity curve for the Lonfearn Member at the Shielling Burn, Eigg

As with the North-Shore, Eigg section very few samples were available for comparative study of the fauna. The palaeosalinity of the section was in general oligohaline to mesohaline (0.5–18‰). The curves derived (Text-fig. 12A–B) from the molluscs and the ostracods do differ. This is because of the presence of the ostracod *Glyptocythere shielingensis* in the *Unio* shell hash. A similar explanation, but in reverse, to that given for Bed 3h from the type section of the Kildonnan Member may be applicable in this instance.

Palaeosalinity curve for the Kildonnan and Lonfearn members, Rudha nam Braithairean, Trotternish, Skye

The Kildonnan Member section is dominated by the ostracods *Linnocythere incerniculum* and *Darwinula pulmo*, the bivalve *Neomiodon brycei*, the conchostracan *Neopolygrapta lealtensis*, the gastropod *Viviparus scoticus*, as well as numerous fish and plant fragments. In all samples *Linnocythere incerniculum* is more abundant than *Darwinula pulmo*, making up 81–97 per cent. of the ostracod fauna (Text-fig. 5). This, combined with the occurrence of the bivalve *Neomiodon brycei* and the conchostracan *Neopolygrapta lealtensis*, indicates a salinity of probably no higher than 10‰.

The ostracod assemblage at the top of Bed 9c is also dominated by *Linnocythere incerniculum* (88 per cent. with a calculated 16230 specimens per kg of sediment) with *Darwinula pulmo* (12 per cent. with a calculated 2290 specimens per kg) subordinate. *Progonocythere milleri* also occurs, making up less than 1 per cent. of the assemblage. A similar level with *Progonocythere milleri* was also found at the type section of the Kildonnan Member (Bed 6b) and in the Kildonnan Member from the North-Shore Section, Eigg (Bed 7). It was suggested by Wakefield (1991, 1994) that *Progonocythere milleri* be used as a marker fossil to enable correlation between the different sections of the Kildonnan Member. In the context of this paper *Progonocythere milleri* indicates an area-wide increase in salinity. This salinity event is only fully recognized in the North-Shore Section, Eigg where both sexual dimorphs and three juvenile stages are preserved, indicating that it was *in situ* and that energy conditions were moderately high as compared with the rest of the section.

The occurrence of *Progonocythere milleri* towards the top of the Kildonnan Member was not the only area-wide faunal event experienced during the deposition of the Lealt Shale Formation. The Algal Bed itself was used as evidence for the area as a whole, the Sea of the Hebrides and Inner

Hebrides basins of Binns *et al.* 1975, acting as one (Hudson 1970, 1980). Immediately above the Algal Bed (basal 50 mm of Bed 1, Lonfearn Member) at Rudha nam Braithairean the ostracod fauna consists of *Glyptocythere dextranovacula*, *Glyptocythere sutherlandi*, *Aalenella cuneata* and *Lophocythere* sp. A, with the bivalve *Neomiodon brycei*. The absence of the ostracod *Linnocythere spinosa* indicates that the salinity was probably above 15‰. Certainly, immediately above the basal 50 mm of Bed 1, the salinity had probably increased to 15–20‰. The fauna here contains the same ostracods but the bivalve *Neomiodon brycei* is subordinate to the bivalve *Quenstedtia?* sp. The change in the bivalve fauna indicates a probable slight increase in salinity between the two levels. It is worth noting that the same fauna and presumably salinity range was also found in Bed 1 of the Lonfearn member at the North-Shore section, Eigg (see above).

From the top of Bed 1 onwards the palaeosalinity remains fairly stable; within the oligohaline range (0.5–5‰). *Linnocythere spinosa* and *Darwinula phaseus* dominate the ostracod fauna with numerous conchostracans and, in the base of Bed 3, occur with the planispiral foraminifer *Ammodiscus tenuissimus*.

Occasionally the salinity increased, such as in Bed 7 and at the top of Bed 9; in Bed 7 the salinity was probably around 10‰ as indicated by the presence of the ostracods *Linnocythere spinosa* (21 per cent.), *Darwinula phaseus* (20 per cent.) and *Linnocythere melicerion* (16 per cent.). However, salinities may have been higher (15‰) to account for the presence of *Acanthocythere?* sp. A (31 per cent.) and *Lophocythere* sp. A (9 per cent.). *Acanthocythere?* sp. A was preserved only as carapaces of the adults, both male and female, and one specimen of a presumed A-1 juvenile, no individual valves being present. The absence of large numbers of juveniles suggests that higher energy conditions may have winnowed out the smaller juveniles. Of the other ostracod species in that sample only *Linnocythere spinosa* (12 per cent. of specimens), and *Darwinula phaseus* (15 per cent. of specimens) have any carapaces preserved. The assemblage of *Linnocythere spinosa* contains adults and several juvenile stages, possibly indicating lower energy conditions than does the assemblage of *Acanthocythere?* sp. A. The assemblage from Bed 7 may represent a mixing of ostracods which lived at different times. *Acanthocythere?* sp. A probably inhabited the sediment first, when energy conditions were higher. *Linnocythere spinosa* only inhabited the sediment after energy conditions had decreased, which may explain the differences in age structure between the two species. It is always possible that the two species co-existed, and that their valves were affected differently by the water currents, such that more juvenile stages of *Acanthocythere?* sp. A were winnowed out.

Bed 9 is dominated by the bivalve *Neomiodon brycei* and the ostracod *Glyptocythere dextranovacula*. Salinities of around 15‰ or above are postulated. This occurrence of *Glyptocythere dextranovacula* corresponds with the complete absence of *Botryococcus* at that level (Walton 1988).

The sampled interval of the Lonfearn Member in general appears to have been deposited under oligohaline salinities. This is supported by the sometimes high abundance of *Botryococcus* (up to 76.3 per cent.; Text-fig. 13c) based upon data from Walton (1988) and Riding *et al.* (1991).

CONCLUSIONS

The different major components of the biota from the Lealt Shale Formation can all be used in the interpretation of the palaeosalinity of the depositional environment, albeit with varying degrees of precision. The mollusc/conchostracan fauna used by Hudson (1963a) and Harris and Hudson (1980) provides a coarser measurement of the palaeosalinity than does the ostracod fauna. This is probably due to the smaller number of mollusc species (17) when compared with the ostracods (26 in total; 11 in the Kildonnan Member and 15 in the Lonfearn Member, the ranges of which do not overlap but are essentially complementary). With fewer species available for correlation the accuracy with which relative salinity tolerances can be defined is lower. However, the mollusc and conchostracan fauna has one advantage over the ostracod fauna, in that several species are found in both the Kildonnan and Lonfearn members (see Table 1), and, as such, salinities between the two

members can be compared. The difference in the ability to define small scale salinity fluctuations was particularly evident in Bed 5 from the type section of the Kildonnan Member. The bivalve *Praemytilus strathairdensis* dominated the macrofauna, thus reducing the opportunity to detect subtle salinity changes that lay within its large tolerance range (10–20‰). Several salinity fluctuations were noted when studying the ostracod fauna that only became evident with respect to the bivalve *Praemytilus strathairdensis* when its $\delta^{18}\text{O}$ values were studied. A positive correlation between salinity and $\delta^{18}\text{O}$ values was noted.

The integration of palynofloristic data also provides valuable information. The percentage abundances of *Botryococcus* proved to be especially useful in the context of the present study. A negative correlation between salinity and abundance is evident.

Text-figures 10E and 13D show the palaeosalinity envelopes for the type section of the Kildonnan Member and the section at Rudha nam Braithairean.

The Kildonnan Member was deposited under generally low but fluctuating salinities. It is considered unlikely that totally freshwater conditions were ever established, and oligohaline salinities were probably more normal. Many of the fluctuations noted were extremely rapid, e.g. Beds 3g–3h, 5f–5g and 6d–6e from the type section of the Kildonnan Member, and in some cases were basin-wide.

The junction between the Kildonnan and Lonfearn members represents a major faunal changeover of ostracod species. No species of ostracod occurs in both members. It would appear that this was because of environmental factors. This boundary is represented in all sections of the Lealt Shale Formation by a stromatolitic algal limestone (Hudson 1970, 1980; Harris and Hudson 1980) representing a basin-wide desiccation event with pseudomorphs after gypsum occurring along many of the algal laminations (Hudson 1970). Immediately after the deposition of the algal limestone the basin was inundated by higher salinity waters, 20‰ or above, with a completely different ostracod fauna from that seen before. However, the bivalve fauna does not change so drastically at the same time. Of the dominant bivalves in the Kildonnan Member only *Praemytilus strathairdensis* fails to occur in the Lonfearn Member.

The Lonfearn Member was deposited under similarly low salinities to the Kildonnan Member. Again freshwater conditions are considered to be unlikely, and oligohaline salinities appear to have been ubiquitous. It appears that the large scale and frequent salinity fluctuations noted in the Kildonnan Member were not repeated during the deposition of the Lonfearn Member.

It is considered unwise to rely on faunal compositions alone, without careful examination of hand specimens, which allow the relationship of species to one another to be noted. This became evident during the study of Bed 3h from the type section of the Kildonnan Member. Here the brackish-marine tolerant bivalve *Praemytilus strathairdensis*, though dominating the fauna throughout the bed, was only seen as shell hash in the upper part of the bed. In the shall hash large specimens of the freshwater tolerant bivalve *Unio andersoni* appeared to be *in situ*. The observation immediately alters the inferred palaeosalinity from brackish-marine to freshwater/oligohaline. This change in salinity was not clearly defined using the ostracod fauna because of the freshwater ostracods (*Limnocythere incerniculum* and *Darwinula pulmo*) inhabiting sediment, the shell hash, with abundant brackish water ostracods (*Glyptocythere inversalitera* and *Fronslarvata chamaeleon*) already in it.

The evidence available from these refined palaeosalinity curves does not detract from the open lagoonal palaeoenvironment, with direct seawater–freshwater mixing, envisaged by Tan and Hudson (1974) and Hudson (1980). The positive correlation between the water chemistry ($\delta^{18}\text{O}$ of *Praemytilus strathairdensis*) and palaeosalinity, and similar palaeosalinity curves indicated by both benthic (bivalves, gastropods, conchostracans and ostracods) and planktic (*Botryococcus*) biotas confirms the conclusion of Hudson (1963a, 1980) that salinity was the major control on faunal/floral occurrences.

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REFERENCES

- ALLEN P. and KEITH, M. L. 1965. Carbon isotope ratios and palaeosalinities of Purbeck–Wealden carbonates. *Nature*, **208**, 1278–1280.
- TAN, F. C. and DEINES, P. 1973. Isotopic ratios and Wealden environments. *Palaeontology*, **16**, 607–621.
- ANDERSON, F. W. 1948. Algal beds in the Great Estuarine Series of Skye. *Proceedings of the Royal Physical Society (Edinburgh)*, **23**, 123–142.
- BAZLEY, R. A. B. and SHEPPARD-THORN, E. R. 1967. The sedimentary and faunal sequence of the Wadhurst Clay (Wealden) in boreholes at Wadhurst Park, Sussex. *Bulletin of the Geological Survey of Great Britain*, **34**, 1–174.
- ANDREWS, J. E. 1984. Aspects of sedimentary facies and diagenesis in limestone shale formations of the (Middle Jurassic) Great Estuarine Group, Inner Hebrides. Unpublished Ph.D. thesis, University of Leicester.
- 1985. The sedimentary facies of a late Bathonian regressive episode: the Kilmaluag and Skudiburgh formations of the Great Estuarine Group, Inner Hebrides, Scotland. *Journal of the Geological Society, London*, **142**, 1119–1137.
- 1986. Microfacies and geochemistry of Middle Jurassic algal limestones from Scotland. *Sedimentology*, **33**, 499–520.
- and WALTON, W. 1990. Depositional environments within Middle-Jurassic oyster dominated lagoons: an integrated litho-, bio- and palynofacies study of the Duntulm Formation (Great Estuarine Group, Inner Hebrides). *Transactions of the Edinburgh Geological Society*, **81**, 1–22.
- BARKER, D. 1966. Some British Jurassic and Cretaceous Ostracoda. 3. Ostracods from the Portland and Purbeck beds of the Aylesbury district. *Bulletin of the British Museum (Natural History), Geology series*, **11**, 459–487.
- BARNES, R. S. K. 1980. *Coastal lagoons*. Cambridge University Press, Cambridge, xi + 106 pp.
- BARROW, G. 1908. In HARKER, A. (ed.). The geology of the small isles of Invernessshire. *Memoir of the Geological Survey of Great Britain*, 210 pp., 9 pls.
- BATE, R. H. 1967. The Bathonian Upper Estuarine Series of eastern England, Part 1: Ostracoda. *Bulletin of the British Museum (Natural History), Geology series*, **14**, 21–66.
- BENSON, R. H. 1959. Ecology of Recent ostracodes of the Todos Santos Bay Region, Baja California, Mexico. *Contributions from the Museum of Paleontology, University of Michigan*, **23**, 1–80.
- BINNS, P. E., McQUILLIN, R., FANNIN, N. G. T., KONOCTY, N. and ARDUS, D. A. 1975. Structure and stratigraphy of sedimentary basins in the Sea of the Hebrides and the Minches. 93–102. In WOODLAND, A. W. (ed.). *Petroleum geology and the continental shelf of NW Europe. 1, geology*. Applied Sciences Publications, Barking, 501 pp.
- BRADY, G. S. and ROBERTSON, D. 1870. The Ostracoda and Foraminifera of tidal rivers. Part 1. *Annals and Magazine of Natural History, Series 4*, **6**, 1–33.
- BRANSON, C. C. 1936. New name for a Morrison ostracode genus. *Journal of Paleontology*, **10**, 323.
- 1966. Fresh-water Ostracod genus *Theriosynoecium*. *Oklahoma Geological Survey, Oklahoma Geological Notes*, **26**, 87–96.
- BURNE, R. V., BAULD, J. and DeDECKKER, P. 1980. Saline lake charophytes and their geological significance. *Journal of Sedimentary Petrology*, **50**, 281–293.
- CARBONEL, P. and PEYPOUQUET, J. P. 1979. Les ostracodes des series du bassin de l'Omo. *Bulletin de l'Institut de Geologie du Bassin d'Aquitaine*, **25**, 167–199.
- 1983. Ostracoda as indicators of ionic concentrations and dynamic variations: methodology (Lake Bogoria, Kenya). 264–276. In MADDOCKS, R. F. (ed.). *Applications of Ostracoda*. University of Houston, Department of Geosciences, Houston, 677 pp.
- CHEN PEI JI and HUDSON, J. D. 1991. The conchostracan fauna of the Great Estuarine Group, Middle Jurassic, Scotland. *Palaeontology*, **34**, 515–545.
- COLIN, J.-P. and DANIELOPOL, D. L. 1978. New data on the systematics of the Limnocytheridae (Ostracoda, Cytheracea). *Géobios*, **11**, 563–567.
- 1979. Why did most of the Timiriaseviinae (Ostracoda, Crustacea) become extinct. *Géobios*, **12**, 745–749.
- 1980. Sur la morphologie, la systématique, la biogéographie et l'évolution des ostracodes Timiriaseviinae (Limnocytheridae). *Paléobiologie Continentale*, **11**, 1–51.

- DANIELOPOL, D. L. 1965. Nouvelles données sur les ostracodes d'eau douce de Roumanie: *Cordocythere phreatica* n. g. sp., *Eucypris petkovskii* n. sp., Limnocytherini et Metacyprini nouvelles tribus de la sous-famille Limnocytherinae Sars, 1925. *Annales de Linnologie*, **1**, 443–468.
- DeECKKER, P. 1981a. Ostracods of athalassic saline lakes: a review. *Hydrobiologia*, **81**, 131–144.
- 1981b. Taxonomy and ecological notes for some ostracods from Australian inland waters. *Transactions of the Royal Society of South Australia*, **105**, 91–138.
- 1983. Notes on the ecology and distribution of non-marine ostracods in Australia. *Hydrobiologia*, **106**, 183–220.
- BAULD, J. and BURNE, R. V. 1982. Pillie Lake, Eyre Peninsula, South Australia: modern environment and biota, dolomite sedimentation, and Holocene history. *Transactions of the Royal Society of South Australia*, **106**, 169–181.
- FORESTER, R. M. 1983. Relationship of two lacustrine ostracode species to solute composition and salinity: implications for paleohydrochemistry. *Geology*, **11**, 435–438.
- and BROUWERS, E. M. 1985. Hydrochemical parameters governing the occurrence of estuarine and marginal estuarine ostracodes: an example from south-central Alaska. *Journal of Paleontology*, **59**, 344–369.
- GRAMANN, F. 1971. Brackish or hyperhaline? Notes on paleoecology based on Ostracoda. 93–99. In OERTLI, H. J. (ed.). *Paleoecologie des Ostracodes*. *Bulletin Centre de Recherches du Pau-SNPA*, **5** (suppl.), 953 pp.
- HAGERMANN, L. 1967. Ostracodes of the Tvärminne area, Gulf of Finland. *Societas Scientiarum Fennica, Commentationes Biologie*, **30**, 1–12.
- HARDIE, L. A. and EUGSTER, H. P. 1970. The evolution of closed basin brines. *Mineralogical Society of America, Special Paper*, **3**, 273–290.
- HARRIS, J. P. and HUDSON, J. D. 1980. Lithostratigraphy of the Great Estuarine Group (Middle Jurassic), Inner Hebrides. *Scottish Journal of Geology*, **16**, 231–250.
- HARTEN, D. VAN and HINTE, J. E. VAN 1984. Ostracod range charts as a chronoecological tool. *Marine Micropaleontology*, **8**, 425–433.
- HRS-BRENKO, M. 1978. The relationship of temperature and salinity to larval development in mussels (*Mytilus galloprovincialis* Lamarck). 359–366. In McCLUSKY, D. S. and BERRY, A. J. (eds). *Proceedings of the 12th European Marine Biology Symposium*. Pergamon Press, Oxford, 388 pp.
- HUDSON, J. D. 1962. The stratigraphy of the Great Estuarine Series (Middle Jurassic) of the Inner Hebrides. *Transactions of the Edinburgh Geological Society*, **19**, 139–165.
- 1963a. The recognition of salinity controlled mollusc assemblages in the Great Estuarine Series (Middle Jurassic) of the Inner Hebrides. *Palaontology*, **6**, 318–226.
- 1963b. The ecology and stratigraphical distribution of the invertebrate fauna of the Great Estuarine Series. *Palaontology*, **6**, 327–348.
- 1966. Hugh Miller's Reptile Bed and the *Mytilus* Shales, Middle Jurassic, Isle of Eigg, Scotland. *Scottish Journal of Geology*, **2**, 265–281.
- 1970. Algal limestones with pseudomorphs after gypsum from the Middle Jurassic of Scotland. *Lethaia*, **3**, 11–40.
- 1980. Aspects of brackish-water facies and faunas from the Jurassic of north-west Scotland. *Proceedings of the Geologists' Association*, **91**, 99–105.
- 1990. Salinity from faunal analyses and geochemistry. 406–408. In BRIGGS, D. E. G. and CROWTHER, P. R. (eds). *Palaobiology, a synthesis*. Blackwell Scientific, Oxford, xii + 583 pp.
- in press. Middle and Upper Jurassic of Eigg and Muck. In EMELEUS, C. H. (ed.). *The geology of Rùm and the adjoining islands. Memoir for geology sheet 60 (with parts of sheets 61 and 70), Scotland*. British Geological Survey, London, H.M.S.O.
- and ANDREWS, J. E. 1987. The diagenesis of the Great Estuarine Group, Middle Jurassic, Inner Hebrides, Scotland. 259–276. In MARSHALL, J. D. (ed.). *Diagenesis of sedimentary sequences*. Special Publication of the Geological Society, London, 36. Blackwell Scientific, Oxford, vi + 360 pp.
- and HARRIS, J. P. 1979. Sedimentology of the Great Estuarine Group (Middle Jurassic) of north-west Scotland. 1–13. In *Symposium sur la Sédimentation de Jurassique ouest Européen, Paris, 9–10 May 1977*. Association de Sédimentologues Français, Paris.
- HUTCHINSON, G. E. 1967. *A treatise on limnology. Vol. 2. Introduction to lake biology and limnoplankton*. Wiley, New York, xi + 1115 pp.
- KEYSER, D. 1977. Brackwasser Cytheracea aus Süd-Florida (Crustacea: Ostracoda, Podocopa). *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (Neue Folge)*, **20**, 43–85.
- KILENYI, T. I. and ALLEN, N. W. 1968. Marine brackish bands and their microfauna from the lower part of the Weald Clay of Surrey and Sussex. *Palaontology*, **11**, 141–162.

- and NEALE, J. W. 1978. The Purbeck/Wealden. 299–324. In BATE, R. H. and ROBINSON, E. (eds). *A stratigraphical index of British Ostracoda*. Geological Journal, Special Issue, 8. Seel House Press, Liverpool, 538 pp.
- KNUDSEN, M. 1901. *Hydrograpische tabellen*. Bianco Luna, Copenhagen, 63 pp.
- MANDELSTAM, M. I. 1960. In LJUBIMOVA, P. S., MANDELSTAM, M. I. and SCHNEIDER, G. F. (eds). *Ostracoda: Nadsemeysto Cypracea. Osonory Paleontologii*, 8, 347–365. [In Russian].
- MARTENS, K. 1990. Revision of African *Limnocythere* s.s. Brady, 1867 (Crustacea, Ostracoda), with special reference to the Rift Valley lakes: morphology, taxonomy, evolution and (palaeo-)ecology. *Archiv für Hydrobiologie*, 1 suppl., 83, 453–524.
- MOOK, W. G. 1971. Paleotemperatures and chlorinities from stable carbon and oxygen isotopes in shell carbonate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 9, 245–263.
- MORKHOVEN, F. P. C. M. VAN 1963. *Post-Palaeozoic Ostracoda. Their morphology, taxonomy and economic use*. Elsevier, London, Vol. 1, 204 pp.; Vol. 2, 478 pp.
- NAUMANN, E. 1922. Die Bodenablagerungen des Süßwassers. *Archiv Hydrobiologia*, 13, 97–169.
- NEALE, J. W. 1988. Ostracods and palaeosalinity reconstruction. 125–155. In DEECKER, P., COLIN, J.-P. and PEYPOUQUET, J. P. (eds). *Ostracoda in the earth sciences*. Elsevier, New York, 302 pp.
- OERTLI, H. J. 1971. The aspects of ostracod faunas. A possible new tool in petroleum sedimentology. *Bulletin Centre de Recherche de Pau-SNPA*, 5 (suppl.), 137–151.
- PEYPOUQUET, J. P., CARBONEL, P. and HEINZELIN, J. DE 1979. Les ostracodes indicateurs de l'évolution paléohydrologique des environnements de la fin du Cénozoïque dans la branch orientale du Rift africain. *Bulletin de l'Institut de Géologie du Bassin d'Aquitaine*, 25, 201–219.
- PINTO, I. D. and KOTZIAN, S. C. B. 1961. New ostracods of the family Darwinulidae and the variation in their muscle scars. *Universidade do Rio do Sul, Instituto de Ciências Naturais, Boletim*, 11, 5–64.
- RANTA, E. 1979. Population biology of *Darwinula stevensoni* (Crustacea, Ostracoda) in an oligotrophic lake. *Annals Zoologica Fennici*, 16, 28–35.
- REDEKE, H. C. 1922. Zum biologie der Niederländischen brackwassertypen. (Ein beitrage zur regionalen limnologie). *Bijdragen tot de Dierkunde (Feest Nummer Max Weber)*, 22, 329–335.
- REMANE, A. 1934. Die Brackwasserfauna. *Verhandlungen Deutschen Zoologischen Gesellschaft*, 36, 34–74.
- 1958. Ökologie des brackwassers, die biologie des Brackwassers. 1. *Die Binnengewässer*, 22, 1–216.
- RIDING, J., WALTON, W. and SHAW, D. 1991. Toarcian to Bathonian (Jurassic) palynology of the Inner Hebrides, Northwest Scotland. *Palynology*, 15, 115–179.
- SANDBERG, P. A. 1964. Notes on some Tertiary and Recent brackish-water Ostracoda. *Pubblicazioni Stazione Zoologica de Napoli*, 33, suppl., 496–514.
- SARS, G. O. 1925. An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. 9 (Ostracoda), (Parts 5–12). Bergen Museum, Bergen, 73–208, 64 plates (33–93).
- SHEPPARD, L. M. 1981. Middle Jurassic Ostracoda from southern England and northern France. Unpublished Ph.D. thesis, London.
- SMITH, A. G., BRIDEN, J. C. and DREWRY, G. E. 1973. Phanerozoic world maps. 1–42. In HUGHES, N. F. (ed.). *Organisms and continents through time. Special Papers in Palaeontology*, 12, vi+334 pp.
- STEPHENS, J. M. 1980. The taxonomy and palaeoecology of Ostracoda from the Great Oolite of Oxfordshire. Unpublished Ph.D. thesis. University College of Wales, Aberystwyth.
- TAN, F. C. and HUDSON, J. D. 1974. Isotopic studies of the palaeoecology and diagenesis of the Great Estuarine Series (Jurassic) of Scotland. *Scottish Journal of Geology*, 10, 91–128.
- TASCH, P. 1987. Fossil Conchostraca of the southern hemisphere and continental drift. *Paleontology, biostratigraphy and dispersal. Memoir of the Geological Society of America*, 165, 290 pp., 49 pls.
- TATE, R. 1873. In BRYCE, J. The Jurassic rocks of Skye and Raasay. *Quarterly Journal of the Geological Society, London*, 24, 318–351.
- VÄLINKANGAS, I. 1933. Über der Biologie der Ostsee als Brackwassergebiet. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 6, 62–112.
- WAGNER, C. W. 1957. Sur les ostracodes du Quaternaire récent des Pays-Bas et leur utilisation dans l'étude géologique de dépôts Holocenes. Thèse, Faculté des Sciences Université de Paris, Mouton and Company, The Hague, 259 pp.
- WAKEFIELD, M. I. 1991. Ostracoda (Crustacea) of the Great Estuarine Group (Bathonian, Middle Jurassic), Inner Hebrides, Scotland. Unpublished Ph.D. thesis. University of Leicester.
- 1994. Middle Jurassic (Bathonian) Ostracoda (Crustacea) from the Inner Hebrides, Scotland. *Palaeontographical Society Monograph*, 148 (596), 1–89, pls 1–11.

- WAKEFIELD, M. I. and ATHERSUCH, J. 1990. On *Theriosynoecium conopium* Wakefield & Athersuch sp. nov. *Stereo-Atlas of Ostracod Shells*, **17**, 31–40.
- WALTON, W. 1988. Palynostratigraphy and palynofloras of the Middle Jurassic (Aalenian to Callovian) strata of the Sea of the Hebrides and Inner Hebrides Basins, NW Scotland. Unpublished Ph.D. thesis, University of Sheffield.
- WARE, M. and WHATLEY, R. C. 1980. New genera and species of Ostracoda from the Bathonian of Oxfordshire, England. *Revista Española de Micropaleontología*, **12**, 199–230.
- 1983. Use of serial ostracod counts to elucidate the depositional history of a Bathonian Clay. 131–164. In MADDOCKS, R. F. (ed.). *Applications of Ostracoda*. University of Houston, Department of Geosciences, Houston, 677 pp.
- WHATLEY, R. C. 1983. The application of Ostracoda to palaeoenvironmental analysis. 51–77. In MADDOCKS, R. F. (ed.). *Applications of Ostracoda*. University of Houston, Department of Geosciences, Houston, 677 pp.
- 1988. Population structure of ostracods; some general principles for the recognition of palaeoenvironments. 245–256. In DEDECKER, P., COLIN, J.-P. and PEYPOUQUET, J. P. (eds). *Ostracoda in the earth sciences*. Elsevier, New York, 302 pp.
- and WALL, D. R. 1975. The relationship between Ostracoda and algae in littoral and sub-littoral marine environments. 173–203. In SWAIN, F. M. (ed.). *Biology and palaeobiology of Ostracoda*. *Bulletins of American Paleontology*, **65**, 687 pp.
- WÜRDIG, N. L. 1983. Fresh and brackish-water ostracodes from the east coast of the State of Rio Grande do Sul, Brazil. 591–604. In MADDOCKS, R. F. (ed.). *Applications of Ostracoda*. University of Houston, Department of Geosciences, Houston, 677 pp.
- YIN JIARUN 1991. Stable carbon and oxygen isotopes in Jurassic shells as palaeosalinity indicators. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, **177**, 163–175.

MATTHEW I. WAKEFIELD

Department of Geology
University of Leicester
University Road
Leicester LE1 7RH

Present Address:
British Gas PLC

Gas Research Centre, Ashby Road
Loughborough LE11 3QU

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APPENDIX

Localities and stratigraphy

(1) Kildonnan Member type section, Eigg [NM 495870]. This section is exposed to the north of Kildonnan on the Isle of Eigg. The section is reached by a narrow cliff path and is exposed on the beach at the start of a beach cliff opposite a distinct shelter stone. The section extends for about 150 m along the shore and is variably exposed from year to year as a result of movement of the storm beach. By the use of distinct marker beds Hudson (1966) was able to construct a composite section. A revised version of this is recorded in Appendix 1 of Wakefield (1991) and in Hudson (in press). The upper portion of Bed 8 and the Algal Bed itself can no longer be seen *in situ* at this locality. These beds lay above a low angle slip plane and have, since their initial recording, been eroded away. The section is best visited at low tide.

(2) Allt na h'Airde Meadhonaich, also known as the Shielling Burn, Eigg [NM 497888]. This stream section running from a dolerite sill with plagioclase phenocrysts on the beach records the upper portion of the Lonfearn Member. The section is interrupted by numerous dolerite sills which have strongly baked the shales.

(3) North-Shore, Eigg [NM 469904–475908]. Only the upper part of the Kildonnan Member is exposed, the base of which is probably equivalent to Bed 5 of the type section. The upper part of the Lonfearn Member is heavily disrupted by numerous sills and dykes, 16–17 m of sediments are

exposed with 16·35 m of sills intercalated. The lower part of the Lonfearn section is relatively undisturbed. This section is best visited at low tide.

(4) Rudha nam Braithairean, also known as Brothers Point, Trotternish, Skye [NG 526625]. This section exposes almost the whole of the Lealt Shale Formation but is intruded by numerous sills, one of which is up to 8 m thick. The upper portion of the Kildonnan Member and the whole of the Lonfearn Member are exposed in the cliff and are accessible with care. The majority of the Kildonnan Member is exposed only at low tide.